DEVELOPMENT OF TOMATO PLANTS OVER-EXPRESSING CYTOKININ SYNTHESIS GENE AND CHARACTERIZATION BY PROTEOMIC APPROACH

A Thesis Submitted to
the Graduate School of Engineering and Sciences of
İzmir Institute of Technology
in Partial Fulfillment of the Requirements for the Degree of

DOCTOR OF PHILOSOPHY

in Molecular Biology and Genetics

by
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January 2020
İZMİR

ACKNOWLEDGMENTS

I would like to express my sincere gratitude to my advisor, Prof. Dr. Anne FRARY for giving me opportunity to be involved in research in plant genetics and proteomics area in an independent manner during PhD studies. Besides it was a pleasure for having the opportunity to work with Prof. Dr. Sami DOĞANLAR. Their guidance, encouragement, effort and patience during the process make the completion of that work possible. They made a great impact for shaping not only my thesis studies but also my entire career as a researcher.

I would also like to state my gratitudes to Prof. Dr Sebastien CARPENTIER for giving me the opportunity to work in his group and complete the phenotyping and proteomic studies of my thesis studies in Laboratory of Tropical Crop Improvement and SyBioMa in KU Leuven.

I am also grateful to my colleagues in İzmir Institute of Technology Department of Molecular Biology and Genetics, especially the members of Plant Molecular Breading Laboratory. I would also express my appriation to my friends Dr. Nergiz GÜRBÜZ and Neslihan TEK, for their support and friendship.

I would also like to state my special thanks to Barış YILDIZ, for his support and encouragement during my studies.

Finally, I would like to express my greatest thanks to my parents Semra ŞELALE and Salih ŞELALE for their love, support and patience through my whole life as well as my graduate studies.

ABSTRACT

DEVELOPMENT OF TOMATO PLANTS OVER-EXPRESSING CYTOKININ SYNTHESIS GENE AND CHARACTERIZATION BY PROTEOMIC APPROACH

Cytokinins (CKs) are plant hormones controlling growth and development including cell division and differentiation, apical dominance and delay of senescence. CKs take part in regulation of the abiotic stress response in plants. In this study, transgenic tomato plants overexpressing the *IPT* (CK biosynthetic gene) were developed. Homozygous transgenic plants exhibited a phenotype with reduced plant stature and lost apical dominance. Increased shoot biomass and leaf water content with a reduction in fruit yield were observed in all transgenic lines. Proteomics analysis was conducted to understand high CK response in molecular level. Proteins supporting a strong sink phenotype and vasculature development were upregulated in transgenic lines and reflected the phenotypic changes observed in homozygous plants. Proteins related to stress response such as detoxification enzymes and PR proteins were upregulated in a gradual manner in transgenic lines with the strongest up-regulation in T6 homozygous line indicating the metabolic stress induced by high CK levels. The transgenic plants were tested for drought stress and observed to have improved water use efficiency, antioxidant response and delayed senescence compared to nontransgenic plants. Proteomic analyses from leaf total and nuclear enriched extracts were conducted to understand the molecular basis of improved drought tolerance. Proteins related to photosynthesis and oxidative stress response were the most prominent groups of differentially abundant proteins in the transgenic line under drought, which could contribute to tolerance. Eighteen transcription factors were differentially abundant in the nuclear proteome of drought stressed plants. These transcription factors could control the gene expression contributing to tolerance.

ÖZET

SİTOKİNİN SENTEZ GENİNİ AŞIRI İFADELEYEN DOMATES BİTKİLERİNİN GELİŞTİRİLMESI VE PROTEOMİK YAKLAŞIMLA KARAKTERİZASYONU

Sitokinler (CK) hücre bölünmesi ve farklılaşması, apikaldominansi ve yaşlanmanın geciktirilmesi gibi bitki büyüme ve gelişimini kontrol eden bitki hormonlarıdır. Ayrıca bitkilerde abiyotik cevabın düzenlenmesinde de rol oynarlar. Bu çalışmada, *IPT* genini (CK biyosentez geni) aşırı ifade eden transgenik domates bitkileri geliştirilmiştir. Homizgot bitkilerde kısa bitki boyu ve apikal dominansın kaybı fenotipleri gözlemlenmiştir. Bütün transgenik bitkilerde yeşil aksam ağırlığında ve yaprak su miktarında artış görülürken meyve veriminin düştüğü gözlemlenmiştir. Yüksek CK tepkisinin moleküler düzeyde anlaşılması için proteomik analizler gerçekleştirilmiştir. Homozigot bitkilerdeki fenotipik değişimlere işarat edebilecek kuvvetli depo fenotipi ve iletim dokusu ile ilgili proteinlerin transgenik bitkilerde yüksek miktarda ifadelendiği tespit edilmiştir. Detoksifikasyon enzimleri ve PR proteinleri gibi stres cevabı ile iligili proteinlerin transgenik hatlarda kademeli olarak arttığı görülmüş, en fazlaartış ise T6 homozigot hattında gözlenmiştir, ki bu artış yüksek CK düzeyleri sebebi ile uyarılmış metabolik strese işaret etmektedir. Geliştirilen transgenik hatlar, kuraklık stresi için test edilmişler ve su kullanım verimi, antioksidan cevap ve geciktirilmiş yaşlanma karakteri bakımından transgenik olmayan bitkilere gore daha üsütün oldukları gözlenmiştir. Gelişmiş kuraklık toleransının moleküler düzeyde anlaşılması için yaprak total protein ve çekirdek zenginleştirilmiş özütlerinde proteomik analizler gerçekleştirilmiştir. Fotosentez ve oksidatif stres cevabı ile ilgili proteinler farklı ifadelenen proteinler arasında en öne çıkan gruplardır ve bunların kuraklık toleransı sağlanmasında etkisi olabilir. On sekiz transkripsiyon faktörünün kuraklık stresi koşulları altında farklı miktarlarda ifadelendiği tespit edilmiştir. Bu transkripsiyon faktörleri toleransa katkı sağlayan genlerin ifadelenmesini kontrol edebilirler.

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CHAPTER 1

DEVELOPMENT OF CYTOKININ OVERPRODUCING TOMATO PLANTS AND PROTEOMICS ANALYSIS OF CYTOKININ RESPONSE

1.1. Introduction

1.1.1. Cytokinins

Cytokinins (CKs) are adenine derivatives containing isoprenoid or aromatic side chains and having multiple roles in plant growth and developmental processes either alone or interacting with other hormones (Mok and Mok, 2001). CKs were first identified to be associated with stimulation of cell division and growth (Miller et al., 1995). But with further studies they were shown to be key regulators of plant growth and development, controlling promotion of shoot growth (Werner et al., 2003), apical dominance (Tanaka et al., 2006), fruit and seed development (Marsch and Martínez et al., 2012), inhibition of root growth (Werner et al., 2003), delay of senescence (Rivero et al., 2007) and cell death (Vescovi et al., 2012). CKs also have roles in sink/source relationships (Pelleg et al., 2011), nutrient uptake (Sakakibara et al., 2006), immunity (Choi et al., 2011) and circadian clock (Zheng et al., 2006). Moreover, they take part in the response and tolerance to environmental stress conditions (Argueso et al., 2009, Werner and Schmülling, 2009). The following sections will give information about CK biosynthesis and metabolism, signaling and its roles in plants.

1.1.1.1. CK Biosynthesis and Metabolism

Plant CKs are adenine derivatives with differing side chains attached to the N^6-position of the purine base (Mok and Mok, 2001). Naturally-occurring CKs are grouped into two classes based on their side chains: isoprenoid and aromatic CKs (Mok and Mok, 2001). N^6-(Δ2-isopentenyl)-adenine (iP) derivatives are the isoprenoid CKs and N^6-benzyladenine derivatives are the aromatic CKs (Strnad et al., 1997). CKs can take three forms in plants: free bases, ribosides and glycosides including O- and N glycosides (Haberer and Kieber, 2002). The activities of these three forms differ. Free ribosides are the active form of the CKs, whereas O- and N glycosides have low activity or are inactive forms (Sakakibara, 2006). The most common and well-studied CKs are zeatin (Z) and N^6-(Δ2-isopentenyl)-adenine (iP). Zeatin can be found in two different configurations as trans (tZ) and cis (cZ) depending on the directionality of the hydroxyl group attached to its isopentenyl side chain (Sakakibara, 2006). iP and tZ are the most common and active CK molecules in most plant species including Arabidopsis and tomato, but cZ is the major form in rice (Sakakibara, 2006; Gajdošová et al., 2011). The distribution and abundance of different CK species and their isoforms depend on plant species, developmental stage and tissue, and are strictly regulated by enzymes controlling their biosynthesis, modification and degradation (Bajguz and Piotrowska, 2009).

In plants, the first step of isoprenoid CK biosynthesis is catalysed by conjugation of an isoprenoid group to the N^6 position of the adenine derivatives. Isopentenyl transferases (IPTs) are enzymesthat catalyze the rate-limiting first step of isoprenoid CK biosynthesis by using a prenyl group from dimethylallyl diphosphate (DMAPP) or hydro-xymethylbutenyl diphosphate (HMBDP) to conjugate with either AMP, ADP or ATP to form iP ribotides (Kakimato, 2001). *IPT* is a multigene family of enzymes and there are nine isoforms which are tissue, organelle or developmental stage-specific in *Arabidopsis* (Takei et al., 2001, Miyavaki et al., 2004). IPT1, 3, 4, 5, 6, 7 and 8 use ATP and ADP as isoprenoid acceptors (Takei et al, 2001). IPT1, 3, 5 and 8 are localized in plastids, IPT7 in mitochondria, and IPT2 and 4 in cytosol (Kasahara et al., 2004). During the vegetative stage, *IPT3, 5* and *7* are the highly expressed isoforms of the gene family, whereas *IPT9* has low expression levels (Miyawaki et al., 2006).

tZ CKs are biosynthesized by either isoprenylation of tRNA by IPT2 and 9 (Miyavaki et al., 2006) or Cytochrome P450 Monooxygenase (CYP735), which converts iP ribotides to tZ ribotides (Takei et al., 2004). In contrast, cZ biosynthesis only occurs by isoprenylation of tRNA (Miyavaki et al., 2006). iP or tZ ribotides are converted to ribosides by enzymes in the nucleoside *N*-ribohydrolase family (Kopečná et al., 2013). Active free base forms of CKs are formed by the release of ribotides by Lonely Guy (LOG) family proteins (Kuroha et al., 2009). There are seven LOG isoforms in *Arabidopsis*, which are tissue and developmental stage specific (Kuhora et al., 2019). *LOG4* and *7* are expressed in the shoot apical meristem (SAM) and have roles in SAM maintenance, whereas *LOG3* and *4* are highly expressed in root cambium (Tokunaga et al., 2012). CK biosynthetic pathway is depicted in Figure 1.1.

Active CK levels can be controlled by de-novo synthesis or enzymatic activation/inactivation (Kiran et al., 2012). Riboside and ribotide CKs are storage and transport forms (Kudo et al., 2010). Active CK levels are restricted either by direct degradation of CKs by CK Oxidases (CKXs) (Werner et al., 2006), or glycosylation (O or N), which reversibly or irreversibly deactivate CKs (Brzobohaty et al., 1993; Sakakibara, 2006). Glucosylated CKs are inactive in bioassays. They cannot bind to CK receptors (Spichal et al., 2004). O-glycosylation can take place in the side chains of zeatin (Z) and dehydrozeatin (dhZ) and this reaction is reversible. β-glucosidases can convert O-glycosylated CKs to active forms by removing O-glycosyl groups (Brzobohaty et al., 1993). However, N-glycosylation of CKs is irreversible. Five CK glucosyl transferases were identified in *Arabidopsis*, two of them encode N-glucosyl transferases and three encode O-glucosyl transferases (Hou et al., 2004). CKXs cleave the unsaturated N6-side chains of isoprenoid CKs and irreversibly inactivate them (Schmülling et al., 2003). *Arabidopsis* encodes seven CKXs isoforms with distinct expression patterns, enzymatic properties and intracellular localizations (Kowalska et al., 2010). Overexpression of *CKXs* causes reduction in CK levels and changes in phenotype (Werner et al., 2003), whereas *ckx* double mutants exhibit phenotypes associated with increased CK levels (Werner et al., 2006).

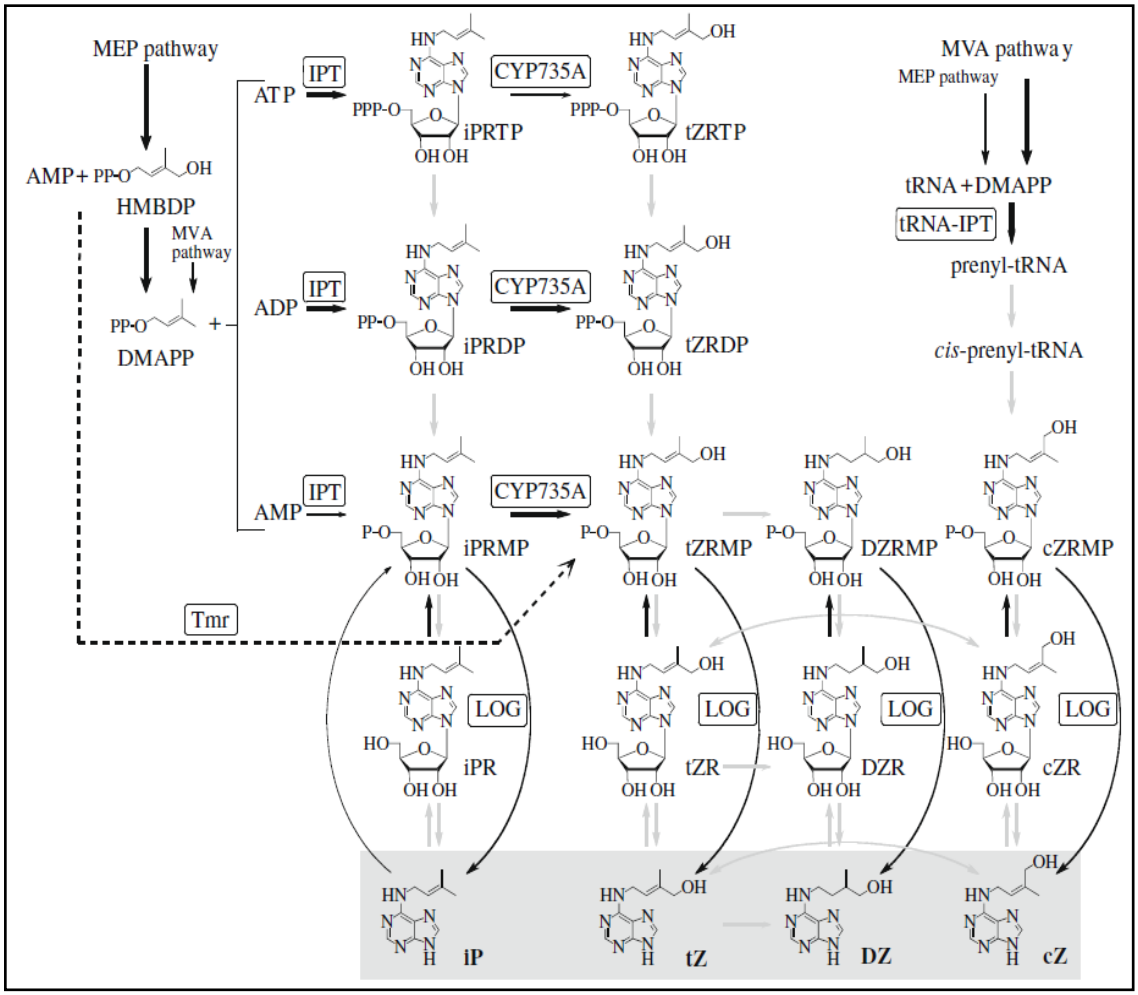

Figure 1.1. Model of isoprenoid CK biosynthesis and metabolism in higher plants. Isoprenyl groups of HMBDP or DMAPP are conjugated with ATP, ADP or AMP via IPT to form iPMP, iPDP or iPTP. iP nucleotides are converted to tZ-nucleotides by CYP735A. di- or tri-phosphorylated CK-nucleosides can be dephosphorylated by phosphatases. tRNA IPTs prenylate tRNA to form cZRMP. LOG cleaves the riboside groups to form active free bases.cZ or tZ can be converted to each other by cis-trans isomerase. Adenosine kinase and phosphoribosyl transferase conjugate phosphoribosyl moieties into iPR and iP respectively. The figure is taken from Kamada-Nobusada and Sakakibara (2009).

1.1.1.2. CK Transport

CKs can be synthesized in different tissues and cell types and then transported to their place of action via local or long distance transport (Kamada-Nobusada and Sakakibara, 2009). tZ type CKs are transported from roots to shoots via xylem and iP type CKs are transported from shoot to roots via phloem (Kudo et al., 2010). Nitrate

causes an increasein IPT3 transcriptionresulting in more tZ type CK in root tissue from where it is transported to shoot tissue via xylem to regulate shoot growth in accordance with nutrient availability (Miyawaki et al., 2004). The ABCG14 transport protein was identified to be related to xylem loading of tZ type CKs in root tissue (Zhang et al., 2014). Disruption of ABCG14 resulted in reduction of CKs in xylem sap and abnormalities in shoot growth associated with reduced CK levels (Ko et al., 2014). The CK signaling pathway is not induced in the cells in which it is synthesized, suggesting that CKs act in a paracrine way (Zürcher et al., 2013). *IPT5* and *LOG4* expression are high during lateral root development in primordial founder cells, but primordial founder cells lack the CK response (Chang et al., 2015). CKs cannot be transported into cells via free diffusion, but are taken into cells via equilibrative nucleoside transporters (ENTs) (Hirose et al., 2005). ENT members are expressed in vascular tissue, suggesting that CK transport could be mediated by them (Hirose et al., 2005). Purine permeases (PUP) are another family of transporter proteins executing CK translocation into the cell. They are not specific to CKs but can translocate adenine and adenine derivatives (Bürkle et al., 2003). Different isoforms of PUP family proteins were identified in different cellular membranes. If localized to the plasma membrane they can mediate CK uptake into cells, or into the phloem to facilitate shoot to root transport. However if PUPs are localized in internal membranes, they could have a role in the sub-cellular distribution of CKs. PUP14 was identified to be localized in the plasma membrane and have a role in the transport of CKs from the apoplast (Zürcher et al., 2016).

1.1.1.3. CK Signalling

The CK response not only depends on the amount of CK available but also on how the CK is perceived and the efficiency of signal transmission into the cell. CKs are sensed and the CK signal is transduced inside the cell via a multistep phosphorelay signal transduction pathway, which is similar to a bacterial two-component signaling system (Stock et al., 2000). Membrane-localized receptor kinases sense the environmental signal whichis amplified by response regulators by further phosphorylation reactions and causes direct regulation of gene expression. Multistep

phosphorelay starts with the autophosphorylation of histidine kinase (HK) subunits by CK binding, then recognition of this phosphorylated HK domain by histine phosphotransferases (AHP) and phosphorylation of AHP by HK, and finally phosphorylation of response regulators (RRs) (Schaller et al., 2011). HKs are found as dimers and they contain CHASE (cyclases/histidine kinases-associated sensing extracellular) domains for CK binding, which face the extracellular space. These proteins also contain histidine kinase and receiver domains localized in the cytosol (Nishimura et al., 2004). A small proportion of HKs localize in the plasma membrane, a significant number of HKs localize in the endoplasmic reticulum (ER) membrane with the CHASE domain oriented through the ER, which means significant CK binding takes place in ER lumen (Wulfetange et al., 2011). CK binding to the CHASE domain causes conformational changes.As a result it activates a His kinase domain on the opposite side of the membrane and autophosphorylation of conserved His and transfer of a phosphoryl group into Asp inside the receiver domain (Ueguchi et al., 2001). The phosphoryl group is transferred to AHP proteins, then to type-B RR proteins, causing positive CK signalling by changing gene expression in the nucleus (Hwang and Sheen, 2001).

AHPs are the second step of CK signalling, and transfer the phosphoryl group from the receiver domain of HKs to the receiver domain of RRs (Hutchison et al., 2006). AHPs are positive regulators of CK signalling (Hutchison et al., 2006). AHPs contain a conserved cysteine residue, which can be S-nitrosylated by nitric oxide, a posttranslational modification that inhibits its phosphoryl group transfer activity from HK to RRs (Feng et al., 2013). Plants contain pseudo phosphotransfer proteins (PHPs), which lack phosphotransfer activity and act as negative regulators of CK signalling (Shaller et al., 2008).

There are two subgroups of RRs: type-A and type-B. Type-B RRs are activated by the transfer of a phosphoryl group in AHPs and act as transcription factors for the induction of the transcriptional response of the CK signalling pathway (Ishida et al., 2008). Many CK-regulated genes contain cis-regulatory elements for type-B RR binding (Hosoda et al., 2002). The turnover rate of type-B RRs is regulated by E3-ubiquitin ligases, which target them for proteasomal degradation (Kim et al., 2012). Some Type-B RRs activate CK response factors (CFRs), which also serve as transcription factors acting parallel to type-B RRs for the exhibition of the CK response (Rashotte et al., 2006). Type-A RRs are negative regulators of CK signalling. Although

they contain a receiver domain for phosphoryl transfer, they do not contain a DNA binding domain for transcriptional regulation. Type-B RRs bind the promoters of type-A RRs and induce their expression (D'Agostino et al., 2000). Type-A RRs are also regulated by different factors such as auxin. For instance, *ARR7* and *15* are repressed by auxin in the shoot apical meristem, however, induced in the root apical meristem (Müller and Sheen, 2008). Ck signalling pathway is depicted in Figure 1.2.

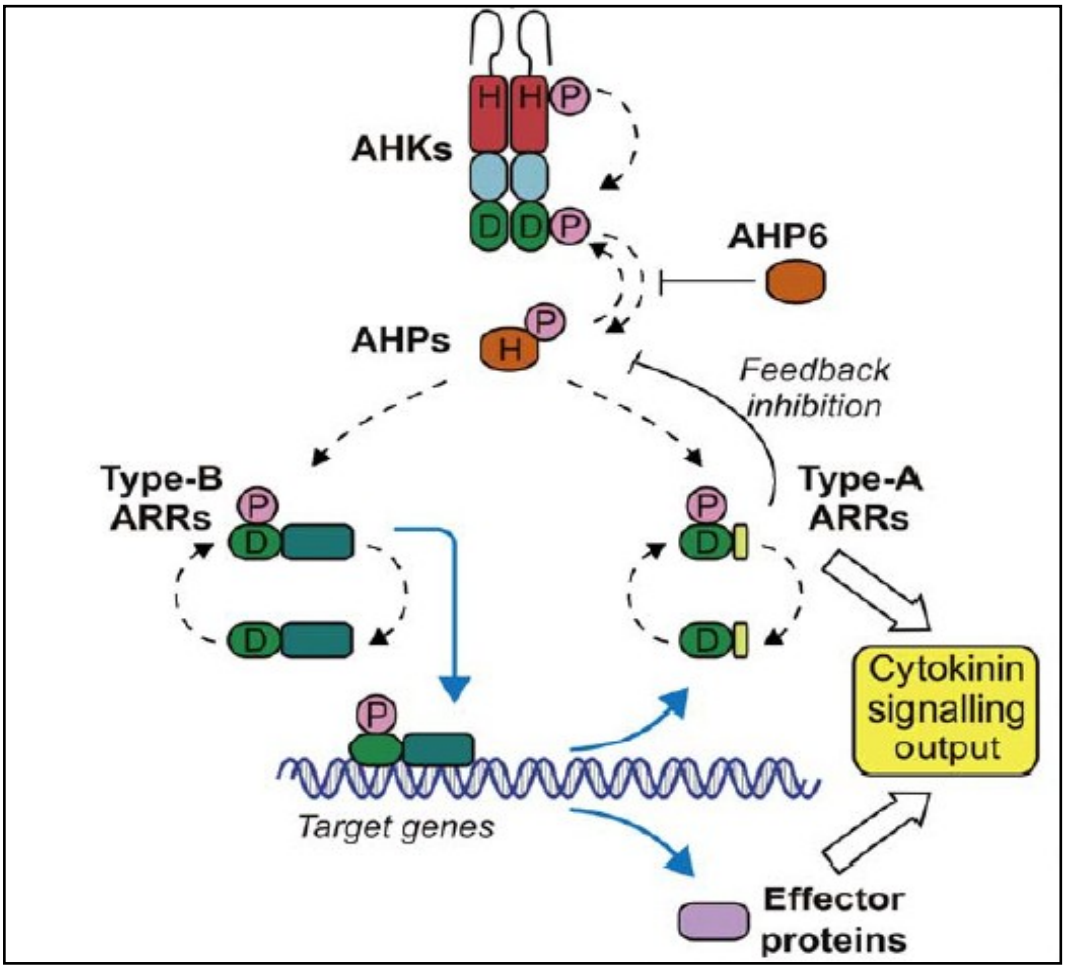

Figure 1.2. Schematic model of CK signalling pathway in plants. CK binding to the AHK CHASE domain activates the His kinase domain of AHK and autophosphorylation of the protein kinase domain (red), followed by the transfer of that phosphoryl group to the receiver domain (green). AHPs recognize the phosphorylated receiver domain of HKT and a phosphoryl group is transferred to a His residue in AHP. AHPs transfer the phosphoryl group into type B or A RRs. Type B-RRs act as positive and TypeA-RRs act as negative regulators of CK response. Type B-RRs act as transcription factors and bind to DNA and regulate the transcription of genes including Type-A RRs, CKX and CRFs. CK response factors (CRFs) work in parallel to type-B RRs to regulate CK responsive gene expression. Type-A RRs form a negative feedback loop to repress CK signalling. The figure is taken from Werner and Schmülling(2009).

1.1.1.4. Roles of CKs in Plants

1.1.1.4.1. Shoot and Floral Development

High CK and auxin levels induce cell proliferation and cause callus formation.However, when callus is subjected to high cytokinin levels, shoot are regenerated (Skoog and Miller, 1957). CK signalling is required for shoot apical meristem (SAM) development. Reduction of CK signalling results in a smaller SAM (Tokunaga et al., 2012). Moreover, inactivation of ABCG14, which is a shoot to root CK transporter, causes abnormalities associated with low CK levels in SAM (Zhang et al., 2014). PUP14 is required for uptake and accumulation of CKs in SAM (Zürcher et al., 2016). *WUSCHEL* (*WUS*) is a gene required for maintenance of stem cell niche in the SAM organization center (Wang et al., 2017). Type-B ARR binding isrequired for transcription of the *WUS* gene, thus CKs are positive regulators of *WUS* expression (Meng et al., 2017). *wus* and *arr1*,*10*,*11*, and *12* mutants are unable to form shoot tissue, which means that both CK signalling and WUS are required for shoot specification and regeneration (Zhange et. al., 2017). *WUS* expression causes shoot regeneration from callus in hormone-free medium and causes SAM formation in roots (Gallois et al., 2004). WUS acts as a downstream component of CK signalling, which is necessary for proper SAM function (Meng et al., 2017). Moreover, Type-A ARRs are repressed by WUS, thus resulting in increased CK sensitivity in SAM. Type-A ARRs (ARR7 and 15) are repressed by auxin via ARF5 (auxin response factor) (Zhao et al., 2010).

Arabidopsis leaf epidermis pavement cell morphology is also regulated by CKs. This auxin-coordinated process is conducted by *ROP GTPase* expression for control of pavement cell interdigitation (Xu et al., 2010). Increased CK content by dexamethasone induced *IPT* overexpression reduced interdigitation, whereas decreased CK content by dexamethasone induced *CKX* overexpression enhanced pavement cell interdigitation (Li et al., 2013). CKs also control stomata density in leaf epidermal tissue. SPEECHLESS (SPCH) is a transcriptional regulator having a role in asymmetric cell division to control stomatal density in leaf epidermis (Pillitteriand Tori, 2007). SPCH both regulates CK signalling andis affected by CK signalling. CK signalling induces *SPCH* expression, but also induces the expression of type-A *ARR16* and *17*, inhibiting CK signalling (Vatén et

al., 2018). In addition, CKs regulate cell division and serration in the leaf margin. CIN-TCP is a transcription factor thatinduces cell cycle arrest in maturing leaves by induction of jasmonic acid biosynthesis. CIN-TCP binds to ARR16 (type-A RR) to induce its expression, which is a negative regulator of CK signalling (Efroni et al., 2013). Thus, jasmonic acid and CK work antagonistically to determine leaf growth.

CKs also have a role in floral development. Functional mutation of type-2 ARRs (*arr1* and *arr10*) impairs carpel regeneration from callus (Rong et al., 2017). AGAMOUS (*AG*) is a carpel identitydefining gene and AAR1 and 10 act as transcriptional regulators of *AG* and induce its expression. Flower meristems have a determined nature to produce a defined number of flowers; however, SAM generates new tissue by continuous division. In flower meristems, auxin activated auxin response factor 3 (ARF3), represses the *IPT*, *LOG* and *AHK* genes as a result of CK signalling (Liu et al., 2014). CK signalling repression by ARF3 is required for floral determinacy.

CKs also play a key role in female gametophyte development from the gynoecium. CKI (CK insensitive) has a key role in female gametophyte development and encodes a histidine kinase, which can activate CK signalling in the absence of CKs (Hwangand Sheen, 2001).

1.1.1.4.2. Root Development

Root growth after the embryonic phase is maintained by the root apical meristem (RAM). The root apex consists of three regions important for growth: the proximal meristem, transition zone (TZ) and elongation zone (EZ). Mitotic division of root cells takes place in the proximal meristem. The cells are pushed to the TZ and cell differentiation and elongation take place in the EZ (Petrica et al., 2012). Auxin and CKs antagonistically control cell division and differentiation at the RAM (Ioio et al., 2007). Auxin regulates cell division in the proximal meristem and CKs regulate cell differentiation in the TZ. SHY2 is a repressor of auxin target genes, which mediates the action of auxin and CK at the RAM (Ioio et al., 2008). *SHY2* expression is induced by ARR1 (type-B ARR) via CKs in the transition zone. Induction of SHY2 causes reduction of *PIN* (*PIN-FORMED*) expression, responsible for auxin distribution

(Růžička et al., 2009). Moreover, increased CKs cause reduced *LAX1* expression, which is an auxin efflux protein in root vasculature (Zhang et al., 2013). Increased auxin targets SHY1 to ubiquitin proteosome degradation (Gray et al., 2001). *IPT5* gene expression is also repressed by SHY2 for negative regulation of CKs (Ioio et al., 2008). At an early developmental stage, the cell division rate must be higher than the cell differentiation rate for establishment of the meristem. At low levels of SHY2, ARR1 is repressed by gibberellin for the establishment of the RAM. ARR12 facilitate the basal level expression of *SHY2* at that stage. An increase is observed in gibberellin levels, followed by an increase in ARR1, which, in turn, causes an increase in the SHY2 levels facilitating cell differentiation at the RAM (Moubayidin et al., 2010). CK-induced expression of type A *ARRs* causes redistribution of PINs in the RAM (Zhang et al., 2011). CKs limit the expression of *SCR* and *WOX5* in an ARR1 and 12 dependent way in the quiescent center (QC), which is composed of cells with low mitotic activity despite high auxin levels (Zhang et al., 2013). For the preservation of QC activity, *SCR* expression is required, WOX5 is also required for prevention of stem cell differentiation (Sabatini et al., 2003; Sarkar et al., 2007). CKs regulate auxin transport to the RAM, in order to establish high auxin levels in the QC. CKs repress *SCR* gene expression by ARR1 in the RAM. *ARR1* expression causes elevated levels of auxin in the QC via *ASB1* expression, which is an auxin biosynthetic gene, positively regulating *SCR* expression (Moubayidinet al., 2013). This tight regulation ensures a high auxin to CK ratio in the QC for maintenance of its identity.

Lateral root growth is necessary for more nutrient uptake from the soil. Lateral root primordial formation is regulated by the antagonistic interaction of auxin and CKs. Lateral root formation is positively regulated by auxins. Auxin efflux carriers mediate the proper spatial distribution of auxins at the newly emerging lateral root tip. However, CKs inhibit lateral root formation (Li et al., 2006). Lateral root formation is increased in CK deficient mutants (Riefler et al., 2006), but mutants with increased CK sensitivity have decreased lateral root formation (To et al., 2004). Pericycle founder cells substantiate anticlinal cell division for lateral root initiation. Lateral root initiation and patterning is disrupted by a CK effect on pericycle founder cells. CKs regulate the expression and distribution of PIN auxin carriers in roots (Ioio et al., 2008). The perturbation of auxin distribution required for lateral root formation is caused by CKs via altered PIN levels in lateral root founder cells (Bielach et al., 2012). CKs target PIN into lytic degradation vacuoles via endocytic recycling in developing lateral roots

(Marhavyet al., 2011). During lateral root formation, CK signalling is repressed by AHP6 much the same as in protoxylem formation (Moreira et al., 2013). CK regulates auxin flow required for the early stage of lateral root formation.

1.1.1.4.3. Vascular Tissue Development

Vascular tissue transports water and minerals from the root to aerial tissues, however, photosynthetic assimilates are transported from source to sink tissues. Procambium gives rise to the vascular primordium, through periclinal division. Similar to growth from the root and shoot apical meristem, auxin and CK signalling antagonistically control growth in vascular tissue. Mutations causing auxin and CK level perturbations cause severe defects in vascular tissue formation (Yokoyama et al., 2007; Köllmer et al., 2014). Defect in AHK4 causes the *woodenleg* (*wol*) mutation, emphasizing the significance of CK in embryonic vascular development (Bishopp et al., 2011). *wol* mutants exhibit a reduction in the vascular system without phloem and metaxylem, however, they develop protoxylem (Scheres et al., 1995). *ahk*, *ahp* and type B *arr* mutations cause similar defects as in *wol* (Argyros et al., 2008; Hutchison et al., 2006; Nishimura et al., 2004). During embryonic vascular tissue formation, auxin determines the areas for CK synthesis, while CK decreases the PIN1 levels in cell membranes (Marhavy et al., 2014). CK response is most important in phloem and auxin signalling is at its maximum in xylem (Mähönen et al., 2006). This CK-auxin polarization is achieved by CK signalling-mediated *PIN* expression in procambial cells, which directs the auxin flux through the xylem axis creating an auxin maxima in protoxylem. Auxin negatively regulates CK signalling by expression of *AHP6* (Bishopp et al., 2011).

CKs also have a role in cambial activity for stem thickening. Reduction of CK expression by *CKX* mis-expression or *IPT* defects causes decreased radial expansion in stems (Nieminen et al., 2008; Miyashima et al.,2013).

1.1.1.4.4. Chloroplast Development and Maintenance

Different components of CK metabolism and signalling are localized in different compartments of the cell for strict regulation of CK action. Chloroplasts have a significant role in CK action. Four CK IPT (IPT1, 3, 5, 8) enzymes, which catalyze the rate limiting step of isoprenoid CK biosynthesis are localized in the chloroplast, whereas one IPT isoform (IPT4) is localized in the cytosol and another (IPT7) is localized in the mitochondrion (Kasahara et al., 2004). Plastid-localized IPT enzymes use the final product of the methylerythritol phosphate pathway as substrate, whereas the cytoplasmic IPT enzyme uses the prenyl groups of mevalonate pathway products as substrate (Sakahibara et al., 2006). Interestingly, when the *Agrobacterium tumefaciens* T-DNA encoded *IPT* gene is transferred into plant cells it is localized in plastids (Sakahibara et al., 2006). Subcellular localization of IPT3 is determined by farnesylation. Its farnesylated form is localized in the cytosol and catalyzes production of iP-type CKs. Non-farnesylated IPT3 is localized in the plastid and catalyzes production of tZ-type CKs (Galichet et al., 2008). The presence of different IPT isoforms localized in different subcellular compartments with most of them localized in plastids indicates the importance of plastids in CK action.

CKs have roles in the formation and control of chloroplast structure. Plastids of dark-grown plants are morphologically changed into etioplasts. When dark-grown plants are exposed to light, etioplast structure is transformed into functional chloroplasts. If CKs are present during the de-etiolation process, plastids are formed, which are larger, with developed thylakoid structures and lacking prolamellar body. However, in the absence of CKs plastids are smaller and transformation of prolamellar body to thylakoid structure is not observed (Kusnetsov et al., 1998). Under normal light conditions, CK-treated plant chloroplasts contained an increased amount of thylakoids per granum (Farineau and Rousseaux, 1975). Moreover, CK treatment increased starch content and hyperstacking of grana (Criado et al., 2009); whereas reduced CK levels due to *pro35S::CKX1* expression reduced grana stacking and few starch grains were observed in these chloroplasts (Werner et al., 2008). In CK-treated plants more chloroplasts were observed in the leaf cells (Boasson and Laetsh, 1969). CKs

alsoregulate plastid division by controlling the levels of the *plastic divisin 2* (*PDV2*) gene (Okazaki et al., 2009).

CKs regulate the biosynthesis and degradation of chlorophyll which is the key component in photosynthesis. Alanine (ala) is the precursor for chlorophyll through the tetrapyrrole biosynthetic pathway. In etiolated plants, Ala biosynthesis is increased in the presence of CKs via stimulation of glutamyl-tRNA reductase and glutamyl-tRNA synthase (Yaronskaya et al., 2006). POR enzyme catalyzes the synthesis of protochlorophyllide a and conversion of protochlorophyllide a into chlorophyllide a. CK treatment increases the levels of POR mRNA in etiolated plants (Kusnetsov et al., 1998). Moreover, POR enzyme is stabilized in the presence of CKs (Kusnetsov et al., 1998). CKs regulate other chlorophyll biosynthetic genes as well. CK treatment increases the steady-state levels of chlorophyll biosynthetic HEMA1, CHLH, and CHL27 mRNAs in etiolated Arabidopsis plants (Tanaka et al., 2011). Induction of chlorophyll biosynthetic enzymes by CK during the de-etiolation process is mediated by AHK2, 3 receptors and ARR1, 12 proteins (Cortleven and Schmülling, 2015).

The effects of CKs on chloroplast components were also investigated under normal light conditions. Increased CK levels by *proSSU::IPT* expression increased chlorophyll content by 50% compared to wild type (Cortlevenand Valcke, 2012), while reduced CK levels caused by *pro35S::CKX1* expression reduced chlorophyll content by 35% (Werner et al., 2008). In *ahk3* and *cre1 ahk3* double mutants, chlorophyll levels decreased around 75%, but a 60% reduction was observed in *ahk2, 3* mutants (Riefler et al., 2006). Triple type B ARR *arr1, 10, 12* mutants also exhibited a similar phenotype with 50% reduction in chlorophyll levels, which indicated that these ARRs are required for optimal levels of chlorophyll biosynthesis (Argyros et al., 2008). Although chlorophyll synthesis is controlled by CK signalling, a basal level of chlorophyll is maintained even in triple CK receptor mutants, which indicates another mechanism to control chlorophyll levels (Nishimura et al., 2004, Riefler et al., 2006). Based on these studies, the AHK2 and AHK3 receptor kinases activate CK signalling and, downstream ARR1, 10, 12 response regulators further modulate CK responsive gene regulation, causing the distinct CK-related response in chloroplasts.

Both increased and decreased levels of CKs caused by *IPT* or *CKX* expression cause changes in the photosynthetic apparatus in plants (Cortleven and Valcke, 2012). However, no significant change was observed in photosynthetic efficiency by *IPT* or *CKX* expression in the study conducted by Cortleven and Valcke (2012). Expression

levels of different components of the photosynthetic apparatus were differentially regulated by CKs. *CAB* (*chlorophyll a binding protein*) of *PSII* and *RubisCO small and large subunit* genes were upregulated by CKs in different plant species (Ohya and Suzuki, 1991; Chory et al., 1994). In Arabidopsis, more than 100 genes regulated by CKs were identified to be photosynthesis-related (Brenner and Shumulling, 2012). Genes related to the biosynthesis of thylakoid membrane lipids such as monogalactosyldiacylglycerol and digalactosyldiacylglycerol were also upregulated (Yamaryo et al., 2003) in response to CK. Plastid genes related to carbon uptake into chloroplast, RNA splicing and photosystem components were also regulated by CKs (Brenner et al., 2005).

Increased CK levels cause a prominent change in the root transcriptome similar to that which occurs in shoot tissue, especially in expression of chloroplastic genes, which could be an indicator of an identity shift (Brenner and Shumulling, 2012). In meta-analysis of transcriptomics studies for evaluation of increased CK levels, two transcription factors, GATA 1 and CRF2, associated with plastid development were identified to be among the top CK-regulated genes (Bhargava et al., 2013). GATA1 (CGA1) and its paralog GNC (nitrate inducible, carbon metabolism involved or GATA21) are among the most important CK-regulated transcription factors having roles in plastid development, and are type IV zinc finger transcription proteins (Riechmann et al., 2000). Expression levels of GATA proteins show a significant difference between light and dark-grown seedlings (Manfield et al., 2007). CKs induce GATA1 expression in a strong manner and GNC to a lesser extent (Chiang et al., 2012). Overexpression of *GATA1* and *GNC* cause induction of differentiation from proplastids to chloroplasts under normal light conditions (Chiang et al., 2012). Moreover, *GATA1* and *GNC* genes control chlorophyll biosynthetic genes such as *HEMA1* and *GUN4* (Hudson et al., 2011). Thus, GATA1 and GNC transcription factors can regulate the gene expression controlling plastid development in a CK-dependent way. GLK (GOLDEN2 LIKE) is another transcription factor similar to GATA1 and GNC. glk2 double mutants exhibit a phenotype with pale green leaves and small chloroplasts whichare unable to form grana. Moreover, *GLK* overexpression resulted in root greening, which is an indicator of chloroplast development in root tissue (Kobayashi et al., 2012). CFR2 is a CK response factor familyand an AP2/ERF class transcription factor, with a role in the control of plastid division (Rashotteet al., 2006). Overexpression of *CFR2* increased the rate of chloroplast division in a PDV2-dependent

manner (Okazaki et al., 2009). It can be concluded that CKs control plastid division by mediating the expression of *CFR2* and its downstream targets PDV2 and 1.

In addition to causing efficiency related changes in the photosynthetic apparatus, CKs have a protective role over the photosynthetic apparatus under light stress. CKs extend the life of photosynthetic apparatus components by an antioxidant protection-based mechanism (Procházková et al., 2008). Under high light stress, plants with lower CK levels suffer from photoinhibition (Cortleven et al., 2014). So-called photodamage in these plants was caused by impairment of the D1 repair cycle and declined photoprotective system efficiency.

1.1.1.4.5. Leaf Senescence

Senescence is a temporally regulated degenerative program, which is the final step of development (Lim et al., 2007). Plants experience senescence in two steps, mitotic and postmitotic senescence. Mitotic senescence is observed in meristematic tissue by arrest of cell division activity. Postmitotic senescence is observed in organs, which have completed their differentiation and maturation.This processis accompanied by degradation of cellular components, their remobilization into newly growing tissue and finally death of the senescent organs (Lim et al., 2003). During leaf senescence, cellular organelles are sequentially disorganized and cellular metabolism and gene expression change. Breakdown of cellular components is organized in the form of programmed cell death (Yadava et al., 2019). The most prominent change in leaf tissue is the breakdown of chloroplasts, which results in a shift from carbon assimilation to catabolism of chlorophylls and other macromolecules. The exportable nutrients produced as a result of catabolic activity are reallocated into different organs (Lim et al., 2007). A major factor determining leaf senescence is developmental age. However internal and external signals are integrated into age information to regulate the progression of senescence (Woo et al., 2018). Internal signals are hormonal, nutritional and water status-related signals, whereas external signals are environmental stresses such as drought, high/low temperature, salinity and pathogen attack. Environmental stresses can induce premature leaf senescence in exposed plants (Irigoyen et al., 1992).

Although leaf senescence is an evolutionary acquired mechanism and required for development especially for reproduction, premature leaf senescence can cause very severe yield and quality losses in crop plants (Gregersen et al., 2013). Moreover, delayed leaf senescence is correlated with increased crop productivity and yield in different crop plants such as maize, rice, wheat and oilseed (Ding et al., 2007; Fu et al., 2011; Hafsi et al., 2000; Hunkova et al., 2011).

CK levels decreaseduring the progression of leaf senescence (Gan and Amasino, 1996). Moreover, exogenous CK treatment causes delayedleaf senescence (Singh et al., 1992a). *IPT* overexpression controlled by a senescence activated promoter (SAG12) causes retardation in the progression of senescence in mature leaves (Gan and Asimano, 1995). The CK biosynthetic enzymes IPT and CK synthase are downregulated and the CK degradation enzyme CKX is upregulated during leaf senescence, accompanied by low CK levels in senescent tissue (Singh et al., 1992b). SAG12 inducible expression of IPT caused increased activity of cell wall invertase (CWINV), which cleaves sucrose to hexoses which then enter into sink cells via hexose transporters. In this study, longevity of the *IPT* overexpressing leaves was associated with increased CWINV activity. Moreover, *proSAG12::CWINV* overexpression also improved leaf longevity, which could be associated with the changed source/sink relations, and as a result, increased sugar availability in cells expressing CWINV (Lara et al., 2004). It is also known that sugar starvation can induce premature senescence (Van Doorn, 2008).For instance, dark-induced senescence of detached leaves is caused by starvation induced by the absence of photosynthesis and can be reverted by treatment with sugars (Fujiki et al, 2001).

CKs also interact with the maturation and aging-related hormone ethylene for the regulation of senescence progression. SAG12 induced overexpression of IPT inhibited corolla senescence in petunia flowers (Chang et al., 2003). Ethylene levels are not affected by CK overexpression, whereas sensitivity to ethylene is reduced in high CK conditions in petunia plants overexpressing the IPT gene.

As was previously mentioned, changes in chloroplasts are the first sign of the onset of senescence. One important aspect of senescence delay by CKs lies in their effect on chloroplast development and regulation of chloroplast structure and function (Cortleven and Schmülling, 2015). Exogenous CK treatment slows down the changes associated with senescence in the chloroplast such as, reduction of chlorophyll content, plastoglobuli formation, decrease in photosynthetic parameters like CO_2 assimilation

rate, PSII photochemical efficiency (Fv/Fm) and photochemical quenching (Qp). CKs upregulate genes related to biosynthesis and protection, and downregulate SAGs (senescence-associated genes) (Hönig et al., 2018). Moreover, enzymes associated with degradation of chlorophylls are inhibited by CKs such as chlorophyllase, Mg-dechelatase, chlorophyll degrading peroxidizes and pheophytinase (Costa et al., 2005; Sergiev et al., 2007). Exogenous treatment with CK derivatives delayed senescence and upregulated the CK response regulators and CK responsive genes including *ARR4*, *5*, *6*, *7*, *8*, *9*, *15*; *CKX4*; *CRF2*; *CRF5* and genes encoding components of the photosystem II light-harvesting complex (Vylíčilová et al., 2016). *proSAG12::IPT* overexpression in tobacco plants caused delayed leaf senescence and was related to the protection of the photosynthetic apparatus and nitrogen partitioning (Jordi et al., 2010). Overexpression of *proSSu::IPT* caused a 10-fold increase in CK content and leaf senescence was delayed, which could be related to activation of antioxidant enzymes as the levels of glutathione reductase (GR), superoxide dismutase (SOD), ascorbate peroxidase (APX) were increased (Synkova et al., 2006).

In addition to direct changes in CK levels, disrupting CK signalling also causes emergence of premature senescence. For instance, disruption of type-A ARRs causes inhibition of leaf senescence in detached leaves and increased CK sensitivity (To et al., 2004). AHK3 disrupted plants exhibited early senescence and, based on the analysis of two isoforms of AHK, AHK3 was identified to have a major effect for regulation of leaf senescence (Kim et al., 2006). Old leaves of *proSAG12::IPT* tobacco plants performed better in terms of physiological parameters, which could be caused by greater antioxidant protection (Procházková et al., 2008).

1.1.1.4.6. Research Objectives and Work Flow

The aim of this work was investigation of the effects of increased CK levels in transgenic tomato plants overexpressing the *IPT* gene. CKs are one of the key hormones regulating plant growth and development both under normal and adverse environmental conditions. As proteins are the functional molecules implementing the molecular level control of life, understanding the changes in the proteome that accompany phenomena

in living organisms is of great importance for understanding their molecular mechanisms. Our aim was to understand the molecular mechanisms of how CKs regulate plant metabolism at the proteome level. For this aim we developed transgenic tomato lines overexpressing the CK biosynthetic gene IPT under the control of the senescence and maturity induced SARK (senescence associated receptor protein kinase) promoter. We selected two transgenic plants from T0 transformants via PCR and southern blot surveys. Then we measured the IPT transgene expression levels in the selected transgenic plants. Zygosity levels of transgenic plants were determined. The selected transgenic plants were evaluated for their phenotypic characters under normal growth conditions by measuring truss, flower, fruit and leaf numbers; plant height; shoot water content; shoot fresh and dry weights. An association between zygosity levels and phenotypes was detected and both hemizygous and homozygous transgenic plants were used for further analysis. We carried out shotgun proteomic analysis using a LC-MS/MS instrument for elucidation of the CK effect in tomato leaf tissue. We identified and quantified the proteins from nontransgenic and transgenic leaf tissues, then determined the differentially abundant proteins between the nontrangenic and hemizygous/homozygous transgenic lines. We conducted functional annotation and characterization of differentially abundant proteins. Clustering analysis was used for determination of expression pattern differences between groups (nontrangenic and two hemizygous/homozygous transgenic lines) that could be associated with different CK levels. To our knowledge, this is the first report of investigation of the proteomic response in tomato plants overexpressing the I*PT* gene.

1.2. Materials and Methods

1.2.1. Vector Constructs

The *IPT* (*isopentenyl transferase*) gene was obtained from Dr. E. Blumwald, University of California, Davis, USA (Rivero et al., 2007). The gene construct contained the *IPT* gene driven by the SARK (senescence associated receptor protein kinase) promoter with a *nos* terminator. The gene construct was cloned into pBI121

which is a binary vector containing the *nptII* gene as a kanamycine selectable marker (Figure A.1). Heat shock transformation method was used for introduction of the plasmid into *A. tumefaciens* strain LBA4404 (Cheng et al., 1998).

1.2.2. Tomato Transformation

Transformation of tomato cv. Moneymaker (MM) was carried out as described by Frary and van Eck (2005). Briefly cotyledons of 1-week old tomato seedling grown in ½ MS0 medium (½ × MS salts; 100 mg/L myoinositol, 2 mg/L thiamine-HCl, 0.5 mg/L pyridoxine-HCl, 0.5 mg/L nicotinic acid, 1% sucrose, and 0.8% agar, pH 5.8) were cut into two pieces and dipped in a suspension of *A. tumefaciens* transformed with the pBI121 plasmid containing the *IPT* gene construct. Shoot formation was induced in selective regeneration media (1× MS salts, 100 mg/L myoinositol, 1× Nitsch vitamins, 2% sucrose, 0.52% agargel, 300 mg/L timentin, 50 mg/L kanamycin, 2 mg/L zeatin, pH 6.0) after co-cultivation of explants with *A. tumefaciens* for 48 h. Until the shoots were large enough to be transferred into selective root media (1× MS salts, 1× Nitsch vitamins, 3% sucrose, 0.8%, Bacto-agar, 300 mg/L timentin, 50 mg/L kanamycin, pH 6.0), explants were transferred into fresh selective regeneration medium every 3 to 4 wk.To ensure that each transgenic plant was formed as a result of an independent transgenic event, only one shoot was maintained from eachcotyledon explant.

After rooting, T_0 plantlets were transferred to soil and gradually acclimated to normal atmospheric conditions as described in Frary and van Eck (2005). For production of T_1 seeds, T_0 plants were grown and self-pollinated in the greenhouse.

1.2.3. Molecular Characterization of T_0 plants

PCR analysis was conducted for confirmation that *IPT* T-DNA was transferred into T_0 and T_1 plants. CTAB method was used for genomic DNA isolation from leaves of greenhouse grown plants (Stewart and Via, 1993). *IPT* gene specific primers were

utilized for PCR reactions. PCR reactions contained: 2.5 µl 10 × PCR buffer, 0.2 mM dNTPs, 2 mM $MgCl_2$, 100 ng template DNA and 1 U Taq DNA polymerase with a total volume of 25 µl. The reaction started with incubation for 5 min at 94°C followed by 30 cycles of 60s at 94°C, 60 s at 58°C, 60 s at 72°C and a final extension of 5 min at 72°C. Then 0.8% agarose gels were used for separation and visualization of PCR products. In PCR experiments, the *SARK::IPT* plasmid construct was used as positive control. Sequences of the primers used in this work are listed in appendix Table A.1.

Southern hybridization analysis was carried out for verification of transgene insertion into the plant nuclear genome. Young leaves of greenhouse grown plants were used for genomic DNA extraction. *Eco*RI restriction enzyme was used for digestion of a total of 25 µg genomic DNA of each PCR-verified T_0 plant. Digested DNA was separated in 0.8% agarose gel. The gels were blotted to positively charged nylon membrane (Roche, Germany) via capillary transfer method. PCR DIG probe synthesis kit (Roche, Germany) was used for production of DIG (digoxigenin) labelled probe using *IPT* gene specific primer. DIG High Prime DNA labelling and detection starter kit I (Roche, Germany) was used for hybridization, wash and immune detection steps according to the manufacturer's instructions. NBT/BCIP (nitrobluetetrazolium/5-bromo-4-chloro-3-indolyl-phosphate) substrate was used for detection of probe binding to restricted genomic DNA.

1.2.4. Determination of Zygosity Level of Segregating Transgenic Plants Using RT-qPCR

For determination of zygosity level (homozygous plants with two copies and hemizygous plants with one copy of the gene of interest), the *IPT* gene and a reference gene were quantified in genomic DNA using a RT-qPCR method (Wang et al., 2015). We tested T_1 seeds from independent *SARK::IPT* transgenic lines T6 and T19. Two fold difference was expected to be observed between the $2^{-\Delta\Delta Ct}$ of homozygous and hemizygous lines. The 15 µl RT-qPCR reactions were set up using 30ng of DNA, 5.5 µl H_2O, 0.25 µl 10 µg/µl forward and reverse primers and 7.5 µl Maxima SYBR Green/ROX qPCR Master Mix kit. The prepared reactions were run in Applied

Biosystems StepOne RT-qPCRsystem (Thermo Fisher Scientific, USA) using pre-incubation, amplification, melting and cooling steps as recommended by the manufacturer. Standard curves were constructed with reactions containing different concentrations of *IPT*-containing plasmid DNA for IPT_105-267 primers and tomato genomic DNA for the β-tubulin reference gene primers. Zygosity levels were calculated according to the formula $\Delta\Delta Ct = (Ct_{IPT} - Ct_{\beta\text{-tubulin}})_{Sample\ 2} - (Ct_{IPT} - Ct_{\beta\text{-tubulin}})_{Sample\ 1}$ and $2^{-\Delta\Delta Ct}$ (Wang et al., 2015).

1.2.5. Evaluation of Plant Growth and Yield Parameters of Transgenic Plants

For evaluation of plant growth parameters and yield under control conditions, transgenic T1 (T_1_6 and T_1_19) plants and nontransgenicMM plants were grown hydroponically under control [EC (electric conductivity)=2.4 mS/m] greenhouse conditions in rockwool slab matrices. Tomato seeds were sown in rockwool plugs and covered with perlite and wetted with water. After seed germination, rockwool plugs were wetted with ½ strength tomato fertigation solution. Two weeks after germination, rockwool plugs with the plantlets were transferred into bigger rockwool matrices and kept growing for a further two weeks. One week after transfer to bigger rockwool matrices, cotyledons were taken and DNA isolation was carried out from T_1_6 and T_1_19 plants via CTAB DNA isolation protocol for verification of the transgenic plants. For PCR verification, a *SARK::IPT* specific PCR primer was used. PCR verified transgenic T_1_6 and T_1_19 plants were selected and used in the next steps of the experiment. For T_1_6 nine plants were identified to contain transgene and T_1_19 ten plants were identified to contain transgene according to PCR analysis. After 2 weeks, rockwool matrices with selected transgenic and nontransgenic plants were placed into rockwool slabs in the prepared greenhouse compartment. Every 4 days, open flowers were pollinated with mechanical pollinator. Plant height, leaf number, truss number, number of open flowers, number of set fruits, and number of fruits with blossom end-rot were counted weekly to follow plant growth and plant yield. Fruits were harvested every two weeks and number and weight of the fruits were recorded. Experiments were

continued for 4 months and phenotypic and yield parameters evaluated for the plants. Using the data collected, variation and differences between different groups and treatments were evaluated considering plant height, leaf number, fruit number, truss number, total fruit weight, leaf fresh weight and leaf water content. Box plots were drawn with R software (Wickham and Grolemund, 2016) using ggplot2 package for the above mentioned characters to see the variation within the groups and the treatments. Two way ANOVA and Tukey's HSD (honest significant difference) tests were carried out to evaluate the statistical significance of the differences between the groups using R software.

1.2.6. Expression Analyses

RT-qPCR experiments were carried out for determination of the mRNA expression levels of the *IPT* gene. Primers specific to *IPT* were designed using Primer3 software (Rozen and Skaletsky, 1999) according to the principles stated by Thornton et al. (2011), which are suitable for the SYBR Green RT-qPCR method. Reference gene primers *TIP41* (TIP41-like family protein), *CAC* (clathrin adaptor complex medium subunit/endocytic pathway gene), ribosomal protein L2 and ubiquitin were used in our study because they have been shown to be stably expressed in different tomato tissues (Expósito-Rodríguez et al., 2008; Løvdal and Lillo, 2009). Total RNA was extracted from the two independent T_1 *SARK::IPT* transgenic plants (T19 and T6), using the RNeasy plant mini kit (Qiagen, Germany) according to the manufacturer's instructions. For removal of DNA contaminants, DNase (NEB, UK) treatment was carried out and total RNA concentration was quantified using Nanodrop Spectrophotometer (MultiskanGO Microplate Spectrophotometer, Thermo Fisher Scientific, USA). cDNA synthesis was conducted usingThermo Revert AidH Minus First Strand cDNA synthesis kit (Thermo Fisher Scientific, USA) with anchored oligo$(dT)_{18}$ primers with a template total RNA (1μ*g*) according to the manufacturer's instructions. 1:10 diluted cDNA samples were used as templates for setting up RT-qPCR reactions using Maxima SYBR Green/ROX qPCR Master Mix kit (Thermo Fisher Scientific, USA) according to the manufacturer's instructions. PCR reactions (10μl) were carried out with an Applied

Biosystems StepOne RT-qPCR (Thermo Scientific, USA) with a program containing pre-incubation, amplification, melting curve and cooling steps according to the manufacturer's instructions. Relative normalized expression levels were calculated using qBase software (Biogazelle, Belgium).Relative normalized expression levels were plotted in box plots using ggPlot2 package, R software (Wickham and Grolemund, 2016).One way ANOVA and Tukey's HSD (honest significant difference) tests were carried out to evaluate the statistical significance of the differences between the groups using R software.For T_1_6 five hemizygous and four homozygous plants and for T_1_19 six hemizygous and four homozygous plants were used to determine the transgene expression levels.

1.2.7. Leaf Total Protein Extraction, Digestion and Cleaning of Peptides

Total leaf protein extraction was carried out in control MM, homozygous and hemizygous T6 and T19 transgenic lines using phenol protein extraction method (Carpentier et al., 2005). Four biological replicates were used for each tested line grown in control conditions and 150 mg leaf tissue was homogenized and dissolved in ice cold 750 µl extraction buffer [100 mM Tris-HCl pH 8.3, 1 % p/v DTT, 5 mM EDTA, 100 mM KCl, 30% sucrose, %0.1 protease inhibitor cocktail (Sigma, USA)]. Solution was vortexed and an equal volume of ice cold tris-buffered phenol (pH 8.3) was added, vortexed for 10 min at 4^{o}C and centrifuged at 12000 g at 4^{o}C for 10 min. The resulting phenol phases were transferred into new tubes, equal volumes of ice cold extraction buffer added, vortexed for 10 min at 4^{o}C and centrifuged at 12000 g at 4^{o}C for 10 min. The resulting phenol phases were transferred into new tubes and four volumes of precipitation buffer (100 mM ammonium acetate in methanol) were added, briefly mixed and kept at -20^{o}C overnight. The next day, solutions were centrifuged at 12000 g for 60 min at 4^{o}C and supernatant removed from the protein pellet. The protein pellets were washed three times withice cold acetone solution with 0.2% DTT. For each washing step, the samples were kept at -20 ^{o}C for 60 min and centrifuged at 12000 g for 10 min at 4^{o}C. After the washing steps, protein pellets were dried at room temperature

and dissolved in 200 µl lysis buffer (30mM tris, 8M urea, 5mM DTT). Protein concentration was determined using 2D-Quant Kit assay (GE Lifesciences).

Proteins were digested and cleaned prior to LC-MS/MS run. Thus, 20mg protein aliquots were used for digestion with trypsin. Protein samples were dilutedwith 200 mM DTT in solution to reach a final 20 mM DDT concentration and incubated 15 min at room temperature. Then the protein solution was diluted with 500 mM iodoacetamide to reach a final concentration of 50 mM and incubated for 30 min at room temperature in dark. After alkylation with iodoacetamide, the protein solution was dilutedthree-fold with 150 mM ammonium bicarbonate solution and 0.2 mg trypsin was added for 20 mg protein and incubated overnight at 37^{o}C for digestion. Digested protein samples were acidified to a final 0.1% concentration with trifluoroacetic acid. Digested protein samples were desalted using Pierce TM C18 Spin Columns (Thermo Fisher Scientific, USA), as explained in the manufacturer's instructions.

1.2.8. Peptide Separation, Identification and Quantification

Digested and cleaned protein samples (1 mg/5 mL) were injected to UPLC MS/MS system for peptide separation and identification according to the protocol explained by Compos et al. (2016). Samples were first separated in Ultimate 3000 UPLC system (Dionex Thermo Scientific) equipped with an Acclaim PepMap100 pre-column (C18 3 µm−100 Å, Thermo Scientific) and a C18 PepMap RSLC column (2 µm, 50 µm–15 cm, Thermo Fisher Scientific, USA). Chromatographic separation was conducted using a linear gradient of 0–4% buffer B (80% acetonitrile, 0.08% formic acid) for 3 min, 4–10% B for 12 min, 10–35% for 20 min, 35–65% for 5 min, 65–95% for 1 min, 95% for 10 min, 95–5% for 1 min and 5% for 10 min; with a flow rate of 300 µL/min. After peptide separation, LC-MS/MS identification was conducted in a Q Exactive Orbitrap mass spectrometer (Thermo Fisher Scientific, USA) instrument operated in positive ion mode with a nanospray voltage of 1.5 kV and a source temperature of 250°C. Proteo Mass LTQ/FT Hybrid ESI Pos. Mode Cal Mix (MS CAL5-1EA Supelco, Sigma-Aldrich) was used as external calibrant and a lock mass of 445.12003 as an internal calibrant. The instrument was operated in data dependent

acquisition (DDA) mode with a survey MS scan at a resolution of 70,000 (fw hm at m/z 200) for the mass range of m/z 400–1600 for precursor ions, followed by MS/MS scans of the top ten most intense peaks with 2+, 3+, 4+ and 5+ charged ions above a threshold ion count of 16,000 at 17,500 resolution using a normalized collision energy (NCE) of 25 eV with an isolation window of 3.0 m/z and dynamic exclusion of 10 s. Raw data were acquired with Xcalibur 2.2 software (Thermo Fisher Scientific, USA), then converted intomgf files using Proteome discoverer [Version 1.4 (Thermo Fisher Scientific, USA)]. Peptide identification was conducted using MASCOT version 2.2.06 (Matrix Science). The peptide database search used the protein database for *Solanum lycpersicum* (Ensembl Plants; https://plants.ensembl.org/index.html). The parameters for MASCOT search were fragment tolerance of 0.02 Da, carbamidomethyl C as fixed modification, oxidation of M as variable modification, parent mass tolerance of 10 PPM, precursor peptide charge state was 2+ and 3+ and up to one missed cleavage was allowed for trypsin. MASCOT database search results were imported to Scaffold version 3.6.5 and peptide identifications were also conducted with X! Tandem (version: CYCLONE, 2010.12.01.1) for further verification of peptide identification.

Protein abundances were calculated by summing the peptides with MASCOT score higher than 20. Differentially abundant proteins were determined based on two-way ANOVA and Tukey's HSD test conducted in R studio platform. Protein abundances for transgenic homozygous and hemizygous lines were compared with nontransgenic line separately and cumulatively. Moreover, each transgenic line was compared for each zygosity levels separately and cumulatively.

For functional annotation of differentially abundant proteins, we conducted MAPMAN and GO annotation using PANTHER database. Over-representation test was carried out to determine the differentially regulated pathways in our differentially abundant protein dataset.

1.3. Results

1.3.1. Development of Transgenic Tomato Lines and Confirmation of *IPT* Gene Expression

Tomato cv MMcotyledon explants were transformed with *A. tumefaciens* strain LBA 4404 containing pBI121 with the *SARK::IPT* gene construct for development of *SARK::IPT* transgenic plants. A total of 35 independent candidate T_0 transgenic plants were regenerated. Using *SARK::IPT* specific primers in PCR reactions, 6 T_0 trangenic plants from 35 T_0 candidate transgenic plants were verified to contain the*SARK::IPT* gene (Figure 1.3). For verification of copy number and transgene integration into the plant nuclear genome, southern blot analysis was carried out on 4 T_0 plants. EcoRI was used for DNA digestion as it cuts the T-DNA once. Single band patterns were observed in southern blot analysis of all 4 tested T_0 transgenic plants, which is an indicator of single copy transgene integration into the plant nuclear genome (Figure 1.4).

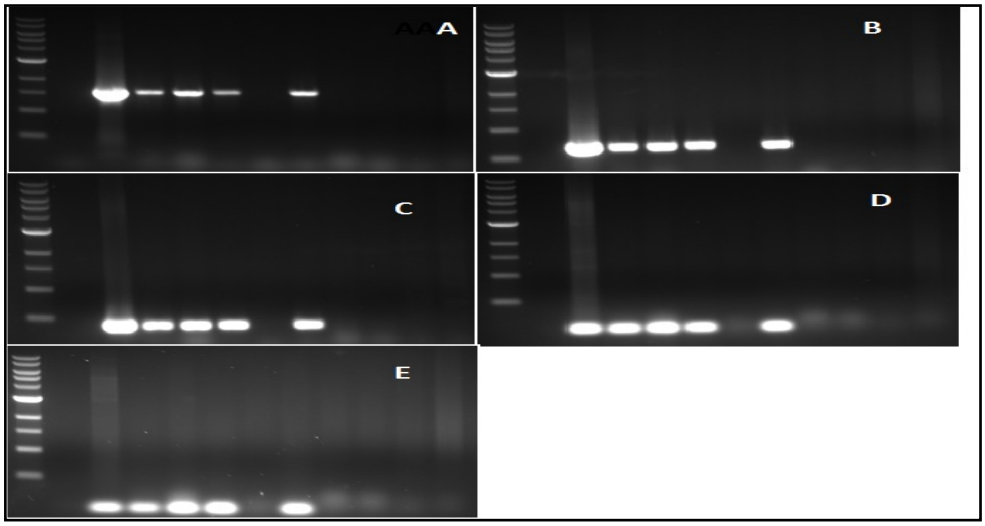

Figure 1.3. Agarose gel image of PCR products of pSICnosKan transformed tomato plants for *SARK::IPT* primers. Gel A: pSARKIPT primers yielding 1.4kb product. Gel B: pSarkF1/iptR1 primers yielding 600bp product. Gel C: iptF2/iptR2 primers yielding 400bp product. Gel D: ipt354/520 yielding 166 bp product. Gel E: ipt105/267 yielding 162 bp product. For each gel: Lane 1 ladder (0.5, 1, 1.5, 2, 3, 4, 5, 6, 8 and 10 kb); Lane 2 negative control with dH_2O; Lane 3 positive control pSICnosKan plasmid; Lanes 4 to 10 were amplification products for DNA from transformed tomato plants. Lane 10 and 11 are non-transformed tomato DNA negative controls. Positive samples were T_0_6, T_0_11 and T_0_19.

Figure 1.4. Detection of T-DNA insertion in the tomato genome by southern blot analysis. Plasmid DNA containing the *SARK::IPT* gene construct was used as positive control and gave a fragment of ~10 kb. PCR positive T_0 plants were tested. EcoRI digested plasmid DNA and genomic DNA were hybridized with DIG labelled DNA probe specific to *SARK::IPT* fragment.

Two of the transgenic T_0 plants were selected for further experiments. T_1 plants and T_2 plants were generated from the T_0 plants by self-pollinating these lines. Transgenic T_1 and T_2 lines were selected by PCR confirmation using *SARK::IPT* gene specific primers (data not shown). RT-qPCR experiments were conducted for these T_1 lines for selection of homozygous and hemizygous plants. For determination of zygosity level (homozygous plants with two copies and hemizygous plants with one copy of the gene of interest), the *IPT* gene and a reference gene were quantified in genomic DNA using a RT-qPCR method. As expected, two fold *IPT* gene expression differences were observed between the $2^{-\Delta\Delta Ct}$ of different lines allowing them to be classified as homozygous or hemizygous for the transgene (Table 1.1).

We tested the *SARK::IPT* expression levels in mature leaf, young leaf and root tissues. As expected, nontransgenic*MM* tomato plants did not show *SARK::IPT* transcription. We observed a significantly higher level of *IPT* expression in mature leaves compared to roots and young leaf tissues. Young leaves of *SARK::IPT_19* had approximately 6 fold lower *IPT* gene expression levels compared to mature leaves,

whereas *SARK::IPT_6* had approximately 3 fold lower expression level. Root tissue of *SARK::IPT_19* had approximately 8 fold lower *IPT* gene expression level compared to mature leaves, whereas *SARK::IPT_6* had approximately 17 fold lower expression levels. Expression also varied between individual transgenic plants. *SARK::IPT_6* had approximately 2.5 fold higher expression levels in mature leaves compared to *SARK::IPT_19* (Figure 1.5). For the proteomics analysis, we selected transgenic line *SARK::IPT_19* because it had lower levels of *IPT* gene expression. The homozygous plants suffered from apex death so we could not take young leaf samples from them, thus *IPT* gene expression data is lacking the homozygous young leaf data.

Table 1.1. Zygosity level calculation for plants grown during greenhouse experiments

Individual	**Ct average(IPT 100)**	**Ct average(b-tubilin)**	**ΔCt**	**ΔΔCt**	**$2^{-\Delta\Delta Ct}$**	**Zygosity**
t6-2	22.88	21.08	1.81	-0.99	1.99	Homozygote
t6-20	23.33	21.56	1.77	-1.02	2.03	Homozygote
t6-34	22.81	20.91	1.89	-0.9	1.87	Homozygote
t6-40	23.34	21.64	1.7	-1.09	2.14	Homozygote
t6-25	23.23	21.48	1.74	-1.05	2.07	Homozygote
t6-29	22.84	20.96	1.88	-0.92	1.89	Homozygote
t6-15	23.44	20.79	2.66	-1.11	2.16	Homozygote
t6-21	23.56	20.9	2.66	-1.1	2.15	Homozygote
t6-12	24.07	21.27	2.8	0	1	Hemizygous
t6-45	24.46	21.69	2.77	-0.02	1.01	Hemizygous
t6-33	24.29	21.47	2.82	0.02	0.99	Hemizygous
t6-11	25.08	22.2	2.88	0.08	0.94	Hemizygous
t6-30	24.23	21.4	2.83	0.04	0.97	Hemizygous
t6-35	24.43	21.9	2.53	-0.27	1.2	Hemizygous
t6-8	24.26	21.51	2.76	-0.04	1.03	Hemizygous
t6-7	25.89	21.81	4.08	0.31	0.8	Hemizygous
t6-9	25.16	21.54	3.62	-0.15	1.11	Hemizygous
t6-10	25.27	21.69	3.58	-0.18	1.14	Hemizygous
t6-38	25.33	21.79	3.54	-0.23	1.17	Hemizygous
t6-41	24.96	21.32	3.64	-0.12	1.09	Hemizygous
t6-43	25.02	21.42	3.6	-0.16	1.12	Hemizygous
t6-3	25.47	21.24	4.24	-0.32	1.25	Hemizygous
t19-2	24.97	20.47	4.5	-1.06	2.08	Homozygote
t19-20	25.9	21.42	4.48	-1.08	2.12	Homozygote
t19-24	25.89	21.4	4.49	-1.07	2.1	Homozygote
t19-34	26.15	21.93	4.22	-1.34	2.54	Homozygote
t19-35	25.46	21.16	4.3	-1.26	2.4	Homozygote
t19-7	27.08	21.71	5.37	-0.19	1.14	Hemizygous
t19-9	26.3	20.97	5.33	-0.23	1.17	Hemizygous

(cont. on next page)

Table 1.1. (cont.)

Individual	Ct average(IPT 100)	Ct average(b-tubilin)	ΔCt	ΔΔCt	$2^{-\Delta\Delta Ct}$	Zygosity
t19-13	27.84	22.19	5.65	0.09	0.94	Hemizygous
t19-17	26.73	21.14	5.59	0.03	0.98	Hemizygous
t19-19	27.68	22.11	5.57	0.01	0.99	Hemizygous
t19-22	27.39	21.83	5.56	0	1	Hemizygous
t19-25	27.05	21.55	5.5	-0.06	1.05	Hemizygous
t19-27	27.07	21.67	5.41	-0.15	1.11	Hemizygous
t19-29	27.31	21.77	5.54	-0.02	1.01	Hemizygous

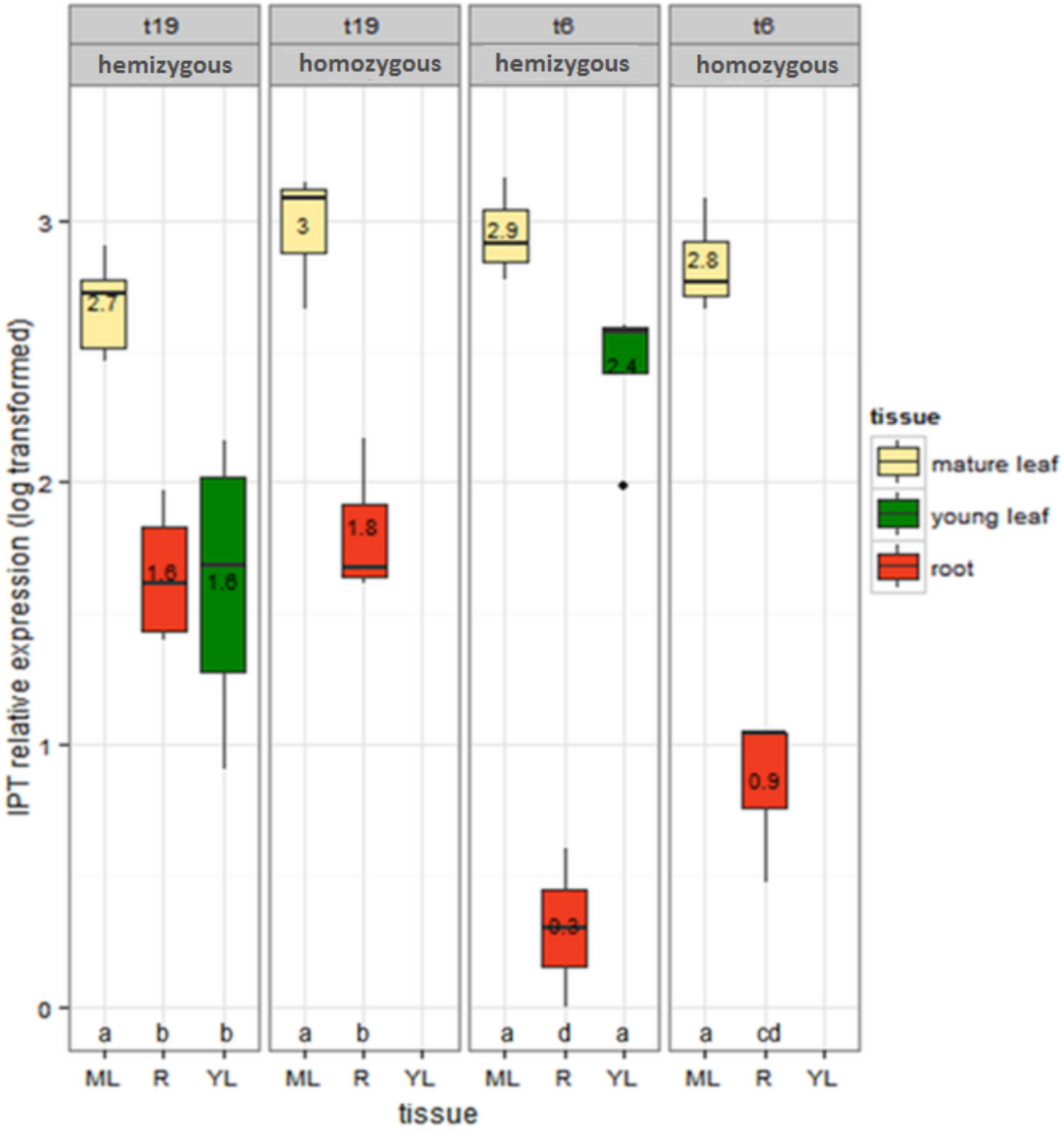

Figure 1.5. Normalized relative mRNA expression levels of *IPT* gene in transgenic tomato plants. ML corresponds to mature leaf, YL corresponds to young leaf, R corresponds to root tissue. Lower case letters indicate statistically significant group differences based on two way ANOVA and Tukey's HSD test.

1.3.2. Evaluation of Plant Growth and Yield Parameters of Transgenic Plants

Homozygous and hemizygous T_1 transgenic plants and the nontransgenic line were grown hydroponically under normal growth conditions and plants were evaluated in terms of growth and yield parameters.We observed symptoms such as necrosis at the edges of newly growing leaves, reduction in plant height (stunted plants) (Figure 1.6), adventitious shoot production from vascular tissue of mature leaves (Figure 1.7) and complete loss of apex/ death (Figure 1.8). Severe symptoms like complete loss of apex and stunted phenotypes were observed in almost one third of transgenic plants which seemed to correspond to the ratio for homozygous plants in our segregating population (homozygous plants without the transgene were eliminated from the population at the seedling stage). Zygosity analysis using RT-qPCR confirmed that the severely affected plants were homozygous for the *IPT* transgene. Reduced performance was observed for all of the examined characters in homozygous transgenic plants with less severe symptoms in hemizygous individuals. Necrosis in young leaves especially at the apex was observed in hemizygous plants at later developmental stage; whereas, in homozygous plants, the apex was completely lost in later developmental stages. Homozygous plants had old leaves that remained green but did not produce any young leaves because of apical death.

A significant increase in plant fresh weight was observed in hemizygous and homozygous T19 lines and in the T6 hemizygous line; with an approximate 1.8 fold increase in the T19 hemizygous and homozygous lines compared to the nontransgenic line and a 1.7 fold in the T6 hemizygous line. Leaf dry weight was also higher than the nontransgenic line in accordance with the leaf fresh weight. There was a significant increase in leaf water content in both hemizygous and homozygous T6 and T19 plants. Increase in water content was around 35% in hemizygous lines and around 50% in homozygous lines compared with the nontransgenic control. Leaf number was significantly reduced in both homozygous lines and in the T6 hemizygote with a 30% reduction in T6 hemizygous and a 50% reduction for homozygous lines. Plant height was significantly reduced in homozygous lines and in the T6 hemizygous line. In T19 hemizygous lines, plant height was similar to the nontransgenic control; however,

approximately 35, 60, and 55% reductionswere observed in T6 homozygous, T6 hemizygous and T19 homozygous lines, respectively.

Figure 1.6. Stunted transgenic plants with apical dominance loss. Left photo with red arrow shows stunted transgenic plant, the other plants were normal growing transgenic plants. Right image shows a close-up of the stunted transgenic plant.

Figure 1.7. Adventitious shoot growth from mature leaf vascular tissue in transgenic plants. Red arrows show the adventitious shoots.

Figure 1.8. T_1 transgenic plants with dying apices. Red arrows show the dying apex tissue.

We did not observe any improvement in plants for fruit yield. Even in control conditions, reductions in fruit yield were observed for both homo- and hemizygous plants (Figure 1.9). Truss number was decreased in all tested transgenic lines except T19 hemizygous individuals compared to the nontransgenic line. Fruit number was also significantly decreased in homozygous lines and in the T19 hemizygous line, whereas the T6 hemizygous line had a similar number of fruits as the nontransgenic control. Even though the T19 hemizygous line had similar truss numbers to the nontransgenic control it had fewer fruits than even the T6 hemizyogous line, which is an indicator of low flower number per truss. The average flower number of trusses in T19 hemizygous

was lower than the nontransgenic and T6 hemizygous lines (data was not demonstrated in the thesis). Total fruit weight was significantly higher for the nontransgenic control than all transgenic lines. An approximate 50% reduction in fruit weight was observed in hemizygous lines. For homozygous lines, the reduction was 60 and 75% for the T19 and T6 lines, respectively. Although the T19 hemizygous line had fewer fruits compared to the T6 hemizygous line, it had greater total fruit weight which indicated heavier fruits compared to T6. Avarage fruit weight of T6 hemizygous and homozygous lineswas reduced around 40% compared to the notransgenic line.

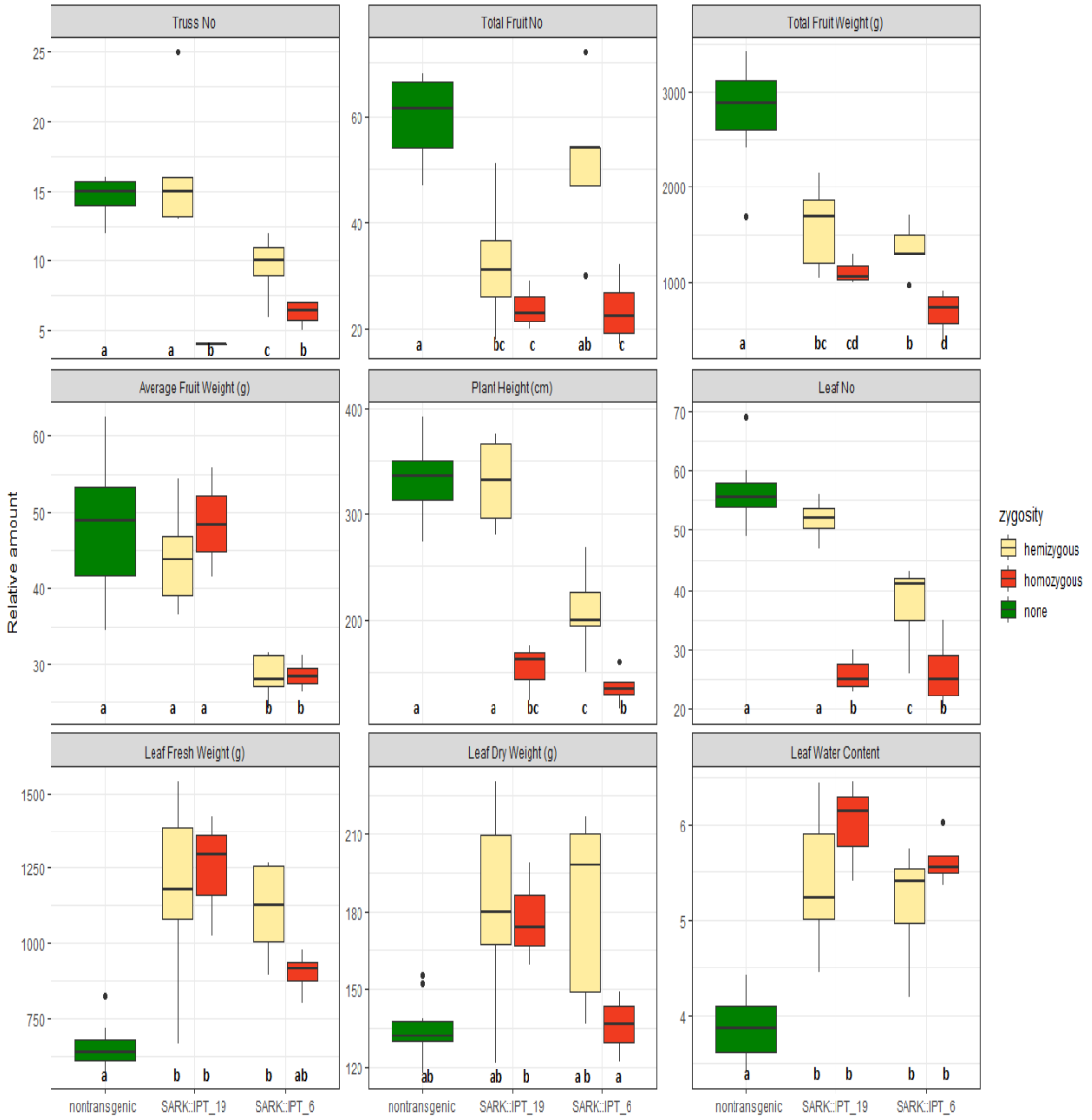

Figure 1.9. Box plots for phenotypic and yield characters of plants grown in greenhouse conditions. Truss number, fruit number, total fruit weight, average fruit weight, plant height, leaf number, leaf fresh weight, leaf dry weight and leaf water contents were evaluated. Lower case letters indicate statistically significant group differences according to Tukey's HSD test.

1.3.3. Leaf Total Proteome Analysis

We conducted proteomics analysis in two independent transgenic lines with different zygosity levels (homozygous, hemizygous) for transgenic (*SARK::IPT*) and nontransgenic MM control plants grown under control conditions for understanding the regulation of cellular metabolism in response to cytokinin overexpression. A total of 5745 peptides were confidently identified with MASCOT scores greater than 20 and 1293 proteins were quantified from leaf total protein samples. A total of 912 proteins were found to be significantly differentially abundant in either T6 homozygous versus nontransgenic, T19 homozygous versus nontransgenic, T6 hemizygous versus nontransgenic,T19 hemizygous versus nontransgenic, T6 homozygous versus T6 hemizygous, T19 homozygous versus T19 hemizygous, T6 homozygous versus T19 homozygous and T6 hemizygous versus T19 hemizygous.

1.3.3.1. Functional Annotation and Classification of the Differentially Represented Proteins

Functional GO term annotation and classification of our datasets were conducted based on PANTHER and Uniprot database analysis. PANTHER Go-Slim biological process analysis were conducted for 912 differentially regulated proteins in either T6 homozygous versus nontransgenic, T19 homozygous versus nontransgenic, T6 hemizygous versus nontransgenic, T19 hemizygous versus nontransgenic, T6 homozygous versus T6 hemizygous, T19 homozygous versus T19 hemizygous, T6 homozygous versusT19 homozygous and T6 hemizygous versus T19 hemizygous and 855 (93.75%) proteins could be assigned to a given function (Figure1.10). The proteins which were differentially abundant in aforementioned test groups the majority of them were associated with metabolic and cellular processes with 356 (41.6%) proteins and 317 (37.1%) proteins for cellular processes and metabolic processes respectively. Other important categories were cellular component organisation with 81 (9.5%) and response to stimulus with 74 (8.7%) proteins. When the molecular process category was

examined in detail, primary metabolic processes (293, 82.3%), nitrogen compound metabolism (129, 36.2%) and biosynthetic processes (106, 29.8%) were the most frequently observed components of that category. When the primary metabolic process category was examined in detail, protein metabolic processes (124, 42.3%) and nucleobase-containing metabolic processes (107, 36.5%) were found to be the major components of that category. When the cellular process category was examined in detail, cell communication (35, 11%) and cell cycle (12, 3.8%) were the major components (Figure 1.11).

Based on PANTHER analysis from the differentially abundant proteins, 613 (67.2%) were assigned to GO Slim molecular functions with the majority, 322 (37.7%) having catalytic activity and 130 (15.2%) having binding activity. The most abundant subcategories in catalytic activity were hydrolase (122, 37.9%), oxidoreductase (95, 29.5%) and transferase activities (65, 20.2%). For binding, the most abundant subcategories were nucleic acid binding (46, 35.4%) and protein binding (45, 34.6%) (Figure 1.12).

The identified differentially abundant proteins were categorized based on GO Slim cellular component categories and 788 (86.4%) of the proteins were assigned into groups (Figure 1.12). Most were assigned to the cell part (339, 39.6%), organelles (232, 27.1%) and macromolecular complex (140, 16.4%). When cell part categories were examined in detail, the intracellular (329, 97.1%) and plasma membrane (26, 7.7%) categories were the major subgroups. When organelle categories were examined in detail, nucleus (49, 21.1%), mitochondrion (38, 16.4%) and plastid (34, 1.7%) were the major subgroups (Figure 1.12).

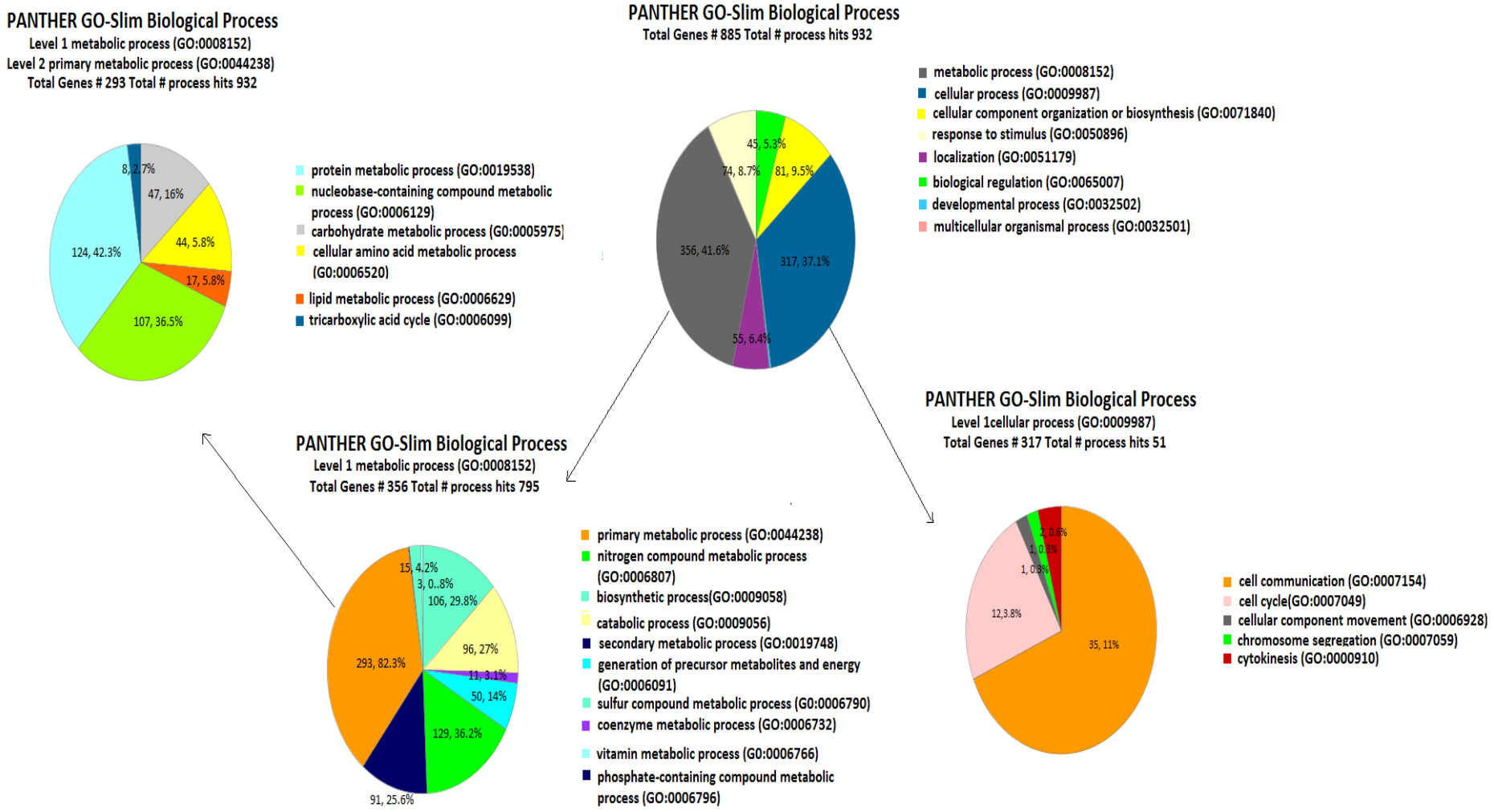

Figure 1.10. Functional classification of differentially abundant proteins based on PANTHER Go-Slim biological process categories in total leaf proteome in response to different zygosity levels of the *IPT* gene.

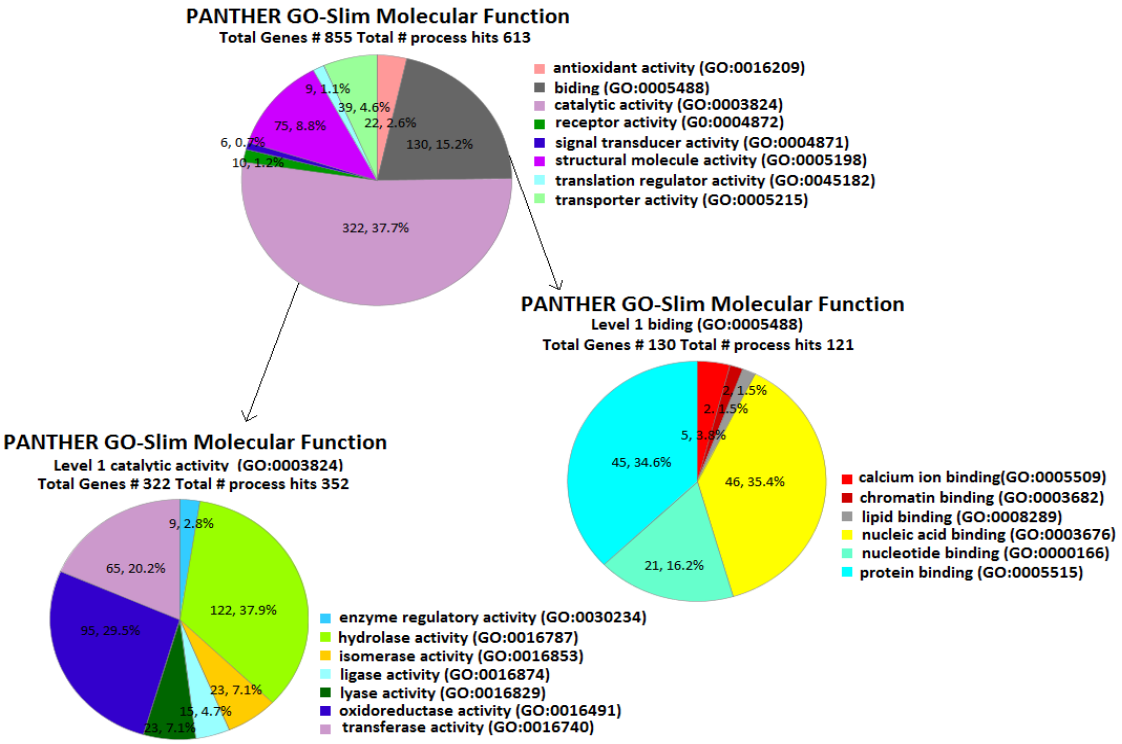

Figure 1.11. Functional classification of differentially abundant proteins based on PANTHER Go-Slim molecular function categories in total leaf proteome in response to different zygosity levels of the *IPT* gene.

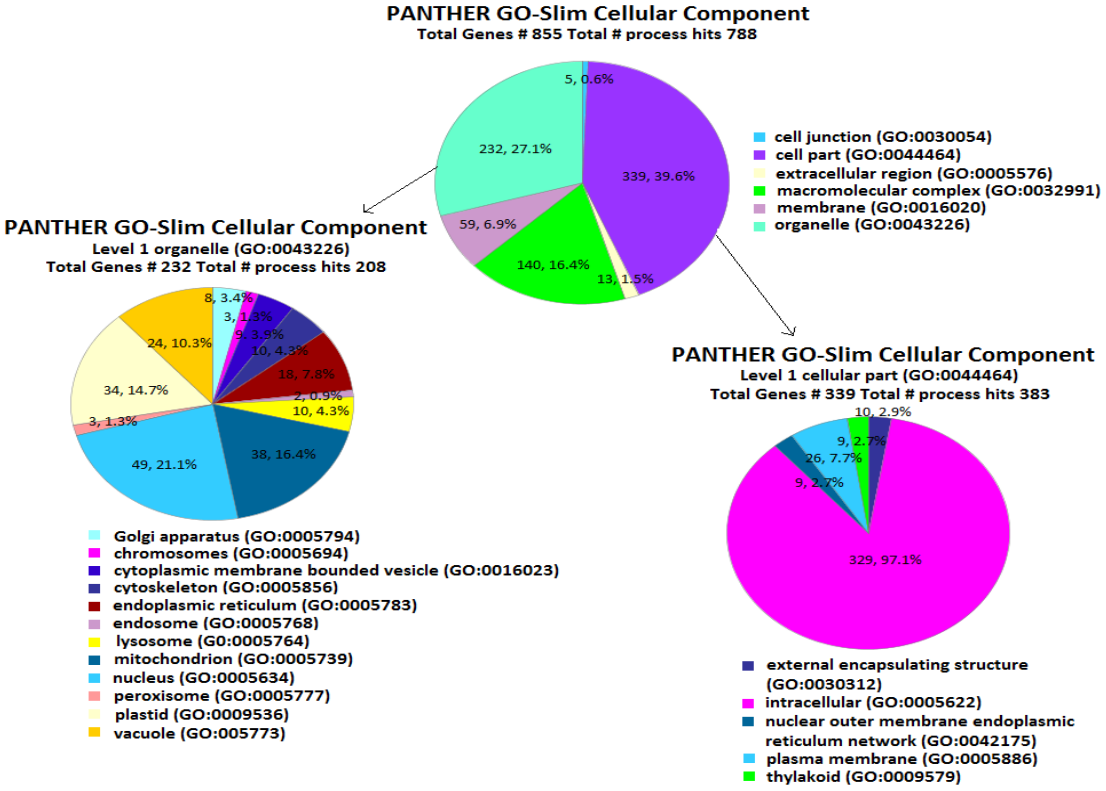

Figure 1.12. Functional classification of differentially abundant proteins based on PANTHER Go-Slim cellular component categories in total leaf proteome in response to different zygosity levels of the *IPT* gene.

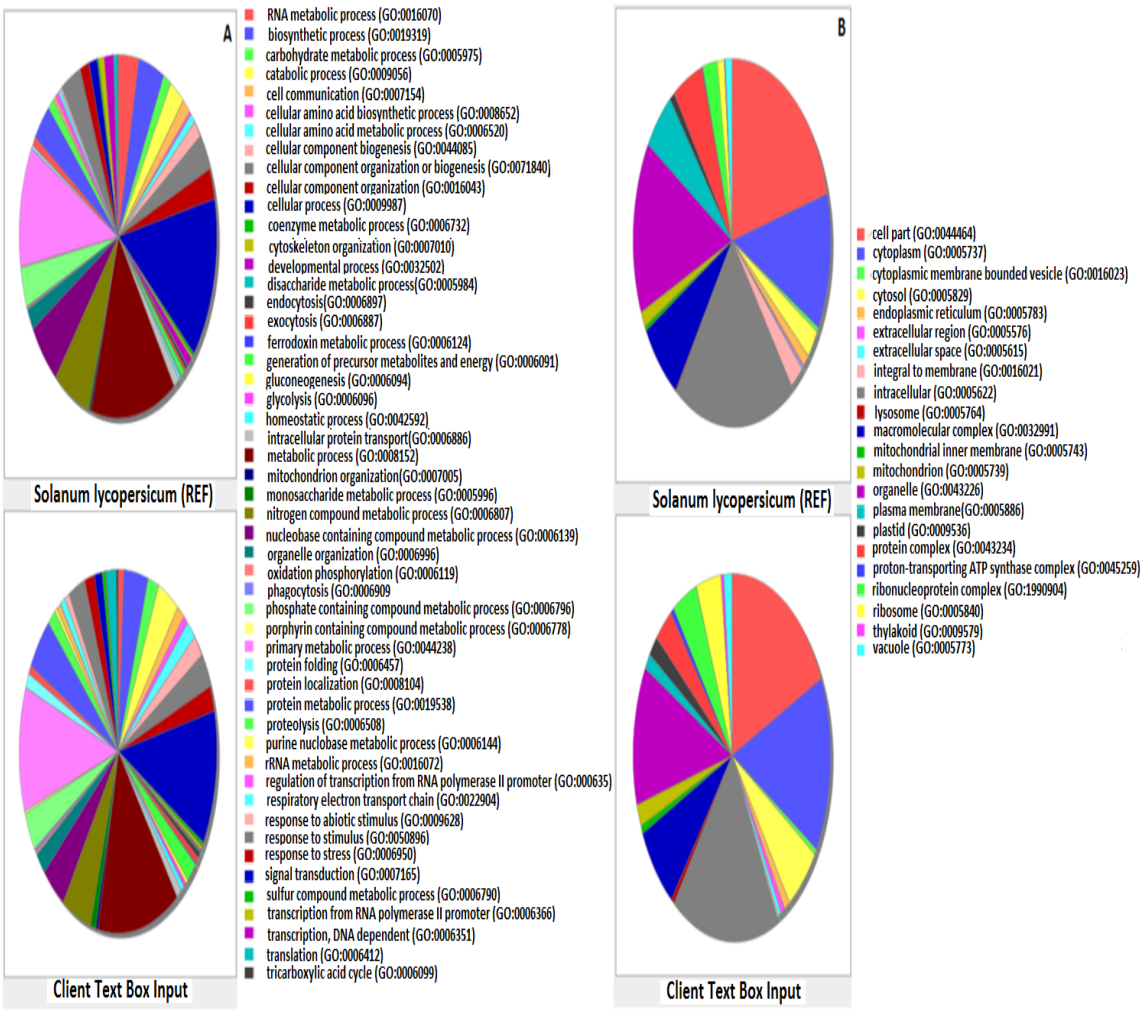

Figure 1.13. PANTHER over-representation tests. A. PANTHER biological process slim over-representation test for leaf total proteome data. B. PANTHER cellular component slim over-representation test for leaf total proteome data.

A functional over-representation test was conducted for understanding which group(s) of proteins were most abundant in our datasets. According to this analysis, the total leaf proteome was enriched in proteins related to glyconeogenesis, glycolysis, tricarboxylic acid cycle and protein folding biological processes with 20.80, 12.13, 9.34 and 8.58 fold over-representation, respectively (Figure 1.13). In a more detailed over-representation analysis based on complete GO biological processes, the enriched proteins were related to glycerol catabolic process (39.71 fold), alditol catabolic process (39.71 fold), photosystem II repair (39.71 fold), photoinhibition (39.71 fold), glyceraldehyde-3-phosphate biosynthetic process (39.71 fold), gravity detection (39.71 fold) and isocitrate metabolic process (39.71 fold). We also conducted a PANTHER GO-slim cellular component based over-representation test to determine which cellular

component accumulated over-represented proteins in our differentially abundant dataset. According to this analysis, the total leaf proteome was enriched in proteins related to the proton-transporting ATP synthase complex, lysosome, ribosome and extracellular component with 11.81, 8.45, 8.18 and 7.35 fold over-representation, respectively (Figure 1.13).

1.3.3.2. PCA Analysis of Proteomics Data

We carried out PCA analysis for the leaf total proteomics data for nontransgenic, T6 homozygous, T19 homozygous, T6 hemizygous and T19 hemizygouslines. In PCA analysis, the T6 homozygous line was located at the far right part of the graph with the T19 homozygous line separated from T6 in the second PC axis.These two lines were separated from rest of the tested lines in the first PC axis (Figure 1.14). From the PCA analysis, we can infer that the T6 homozygote genotype had a more distinct proteomic response than the other tested lines. The T19 homozygotegenotype had the most similar proteomic response to T6 homozygotes. The T6 hemizygous genotype had a proteomic response between T19 homozygous and T19 hemizygous lines. The nontransgenic line exhibited the most distinct proteomics response compared to the T6 homozygotes, while the T19 hemizygous lines exhibited the most similar proteomics response to the nontransgenic line.

PC1 rotations with highest and lowest values are informative for discriminating the homozygous transgenic lines from the nontransgenic and the hemizygous lines. Rotations of PC1 with the lowest values were identified to be proteins downregulated in homozygous T6 alone in both T6 and T19 homozygous lines (Figure 1.15 A). Rotations of PC1 with the highest values were identified to be proteins upregulated in homozygous T6 alone or with the T19 homozygous line (Figure 1.15 B). Most of the proteins with highest rotation values were stress responsive proteins and they were upregulated in homozygous transgenic lines. From the 30 loadings with highest scores for PC1, six were heat shock 70 (HSP70) paralogs, three were cyclophilin paralogs, two were protease proteins, two were mitochondrial ATP synthase subunit proteins, two were toxic carbon metabolism detoxifying enzyme such as formate dehydrogenase and

aldehyde dehydrogenase proteins; two were stress responsive proteins such as chitinase and MLP like proteins; one was a signalling protein RAN3; two were cell organization proteins such as annexin and profilin and one was a glycolytic enzyme, glyceraldehyde-3-phosphate dehydrogenase (Table 1.2). Most of the proteins with the lowest rotation values were photosynthesis related, chloroplast structural and protein metabolism related proteins and they were downregulted in homozygous transgenic lines. From the 30 loadings with lowest scores for PC1, twelve proteins had roles in photosynthesis light reactions, four proteins had roles in photosynthetic Calvin cycle reactions, three had roles as chloroplast structural proteins, one was involved in protein synthesis, three had roles in protein degradation, one was involved in protein posttranslational modification, two proteins had roles in amino acid metabolic processes, one had a role asa stress responsive protein and one was a peroxiredoxin protein (Table 1.2).

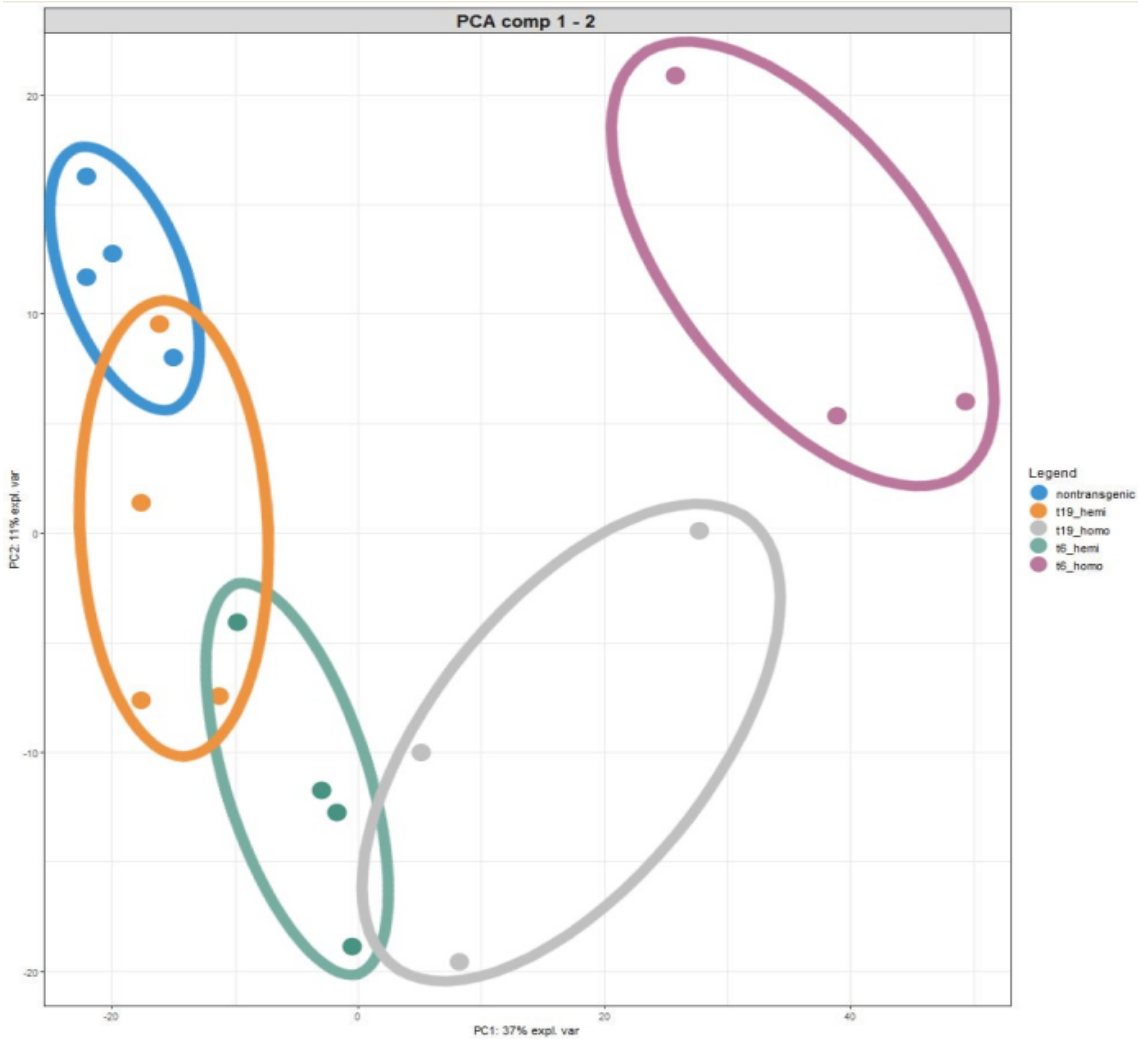

Figure 1.14. PCA analysis for the leaf total proteomics data. Data from each plant is represented by a colored dot as indicated in the legend.

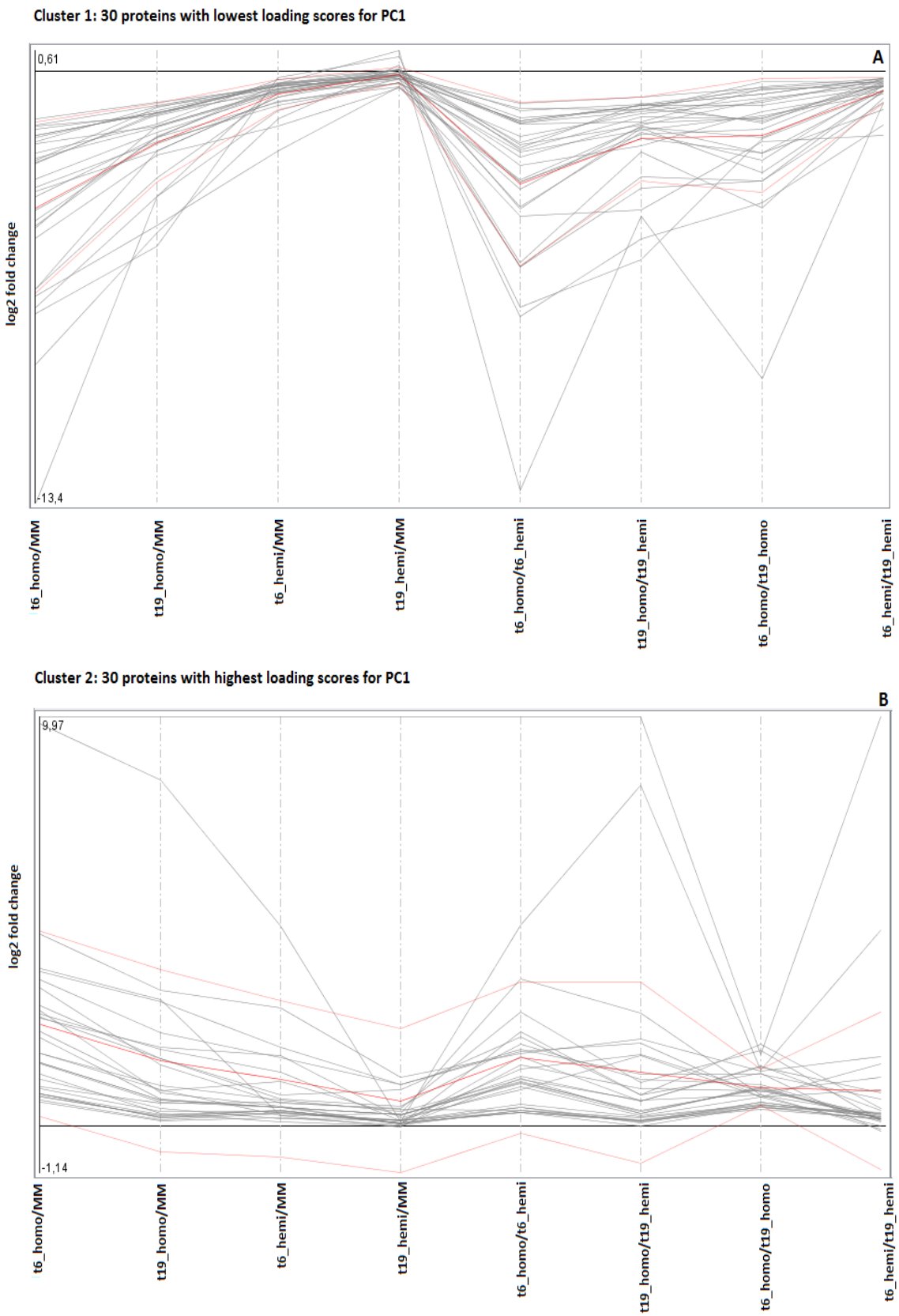

Figure 1.15. Cluster analysis results for proteins with the higest and lowest loading scores for PC1 in PCA analysis. A. Cluster analysis results for proteins with highest loading scores in PC1. B. Cluster analysis results for proteins with lowest loading scores in PC1.

Table 1.2. List of 30 proteins with the highest and lowest loading scores for PC1 in PCA analysis. Fold-differences, p values and MAPMAN bin names are provided.

ID	Description	MAPMAN Category	PC1 Loading Score	homo/MM_fold	homo/MM_Pval	hemi/MM_fold	hemi/MM_Pval	hemi/homo_fold	hemi/homo_Pval
Solyc01g087120.2.1	Uncharacterized protein	mitochondrial electron transport / ATP synthesis.F1-ATPase	0.0439	2.4	1.6E-04	1.5	ns	-0.9	7.4E-04
Solyc08g062920.2.1	Uncharacterized protein	protein.synthesis.elongation	0.0434	1.4	5.8E-04	1.1	ns	-0.3	5.9E-04
Solyc07g005820.2.1	Uncharacterized protein	stress.abiotic.heat	0.0433	1.7	2.8E-04	1.3	ns	-0.4	7.7E-04
Solyc06g072580.2.1	Uncharacterized protein	TCA / org. transformation.TCA.pyruvate DH.E1	0.0433	2.4	7.1E-04	1.1	ns	-1.3	3.6E-04
Solyc04g073990.2.1	Annexin	cell.organisation	0.0431	4.4	2.0E-07	2.5	2.8E-03	-1.9	7.3E-06
Solyc10g086410.2.1	Uncharacterized protein	stress.abiotic.heat	0.043	1.6	7.0E-04	1.2	ns	-0.3	2.0E-03
Solyc11g066060.1.1	Uncharacterized protein	stress.abiotic.heat	0.0429	1.5	7.1E-04	1.3	ns	-0.3	2.6E-03
Solyc06g076970.2.1	Peptidyl-prolyl cis-trans isomerase	cell.cycle.peptidylprolyl isomerase	0.0428	3.1	3.4E-03	1.3	ns	-1.8	2.2E-03
Solyc07g009510.1.1	Uncharacterized protein	stress.biotic	0.0428	10.3	1.3E-05	4.9	ns	-5.6	4.5E-05
Solyc05g023800.2.1	GTP-binding nuclear protein Ran1	signalling.G-proteins	0.0428	1.8	1.4E-06	1.5	5.3E-03	-0.3	1.1E-04
Solyc11g006070.1.1	Peptidyl-prolyl cis-trans isomerase	cell.cycle.peptidylprolyl isomerase	0.0427	3.4	1.5E-04	1.9	ns	-1.5	3.8E-04
Solyc06g076020.2.1	Uncharacterized protein	stress.abiotic.heat	0.0426	1.5	9.1E-04	1.2	ns	-0.3	2.4E-03
Solyc08g066110.2.1	Profilin-2	cell.organisation	0.0426	3.2	1.8E-05	1.6	ns	-1.6	4.0E-05
Solyc07g051850.2.1	Uncharacterized protein	protein.degradation.aspartate protease	0.0426	3.3	3.6E-04	2.2	ns	-1.2	3.7E-03
Solyc11g068510.1.1	Uncharacterized protein	not assigned.unknown	0.0426	1.9	2.0E-03	1.1	ns	-0.8	6.3E-04
Solyc09g010630.2.1	Uncharacterized protein	stress.abiotic.heat	0.0425	1.5	7.8E-04	1.2	ns	-0.3	2.7E-03
Solyc11g066100.1.1	Uncharacterized protein	stress.abiotic.heat	0.0424	1.4	6.4E-04	1.2	ns	-0.2	2.9E-03
Solyc10g005510.2.1	Glyceraldehyde-3-phosphate dehydrogenase	glycolysis.cytosolic branch.glyceraldehyde 3-phosphate dehydrogenase (GAP-DH)	0.0423	3.4	1.8E-04	1.8	ns	-1.6	9.6E-04
Solyc10g077030.1.1	Proteasome subunit alpha type	protein.degradation.ubiquitin.proteasom	0.0423	2.8	2.7E-03	1.7	ns	-1	1.7E-02
Solyc02g086970.2.1	Uncharacterized protein	fermentation.aldehyde dehydrogenase	0.0423	4.5	3.8E-05	1.3	ns	-3.2	1.4E-05

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Table 1.2. (cont.)

ID	Description	MAPMAN Category	PC1 Loading Score	homo/MM_fold	homo/MM_Pval	hemi/MM_fold	hemi/MM_Pval	hemi/homo_fold	hemi/homo_Pval
Solyc06g051650.2.1	Peptidyl-prolyl cis-trans isomerase	cell.cycle.peptidylprolyl isomerase	0.0421	2.6	3.4E-03	1.3	ns	-1.3	2.3E-03
Solyc11g039980.1.1	Uncharacterized protein	PS.lightreaction.ATP synthase	0.0421	1.8	1.4E-03	1.2	ns	-0.7	1.3E-03
Solyc11g007920.1.1	Histone H2B	DNA.synthesis/chromatin structure.histone	0.042	2.2	5.3E-04	1.4	ns	-0.8	1.5E-03
Solyc04g011440.2.1	Heat shock protein 70 isoform 3	stress.abiotic.heat	0.042	1.5	1.7E-03	1.2	ns	-0.3	3.6E-03
Solyc02g038690.1.1	Histone H2B	DNA.synthesis/chromatin structure.histone	0.042	2.2	5.8E-04	1.4	ns	-0.8	1.6E-03
Solyc04g072240.2.1	Uncharacterized protein	not assigned.unknown	0.042	3.7	6.4E-03	1.5	ns	-2.2	6.5E-03
Solyc02g088260.2.1	Uncharacterized protein	not assigned.unknown	0.0419	4.1	1.9E-05	2.4	1.7E-02	-1.7	1.2E-03
Solyc09g005500.2.1	Uncharacterized protein	stress.abiotic.unspecified	0.0418	10	3.9E-04	10	ns	10	6.3E-05
Solyc02g086880.2.1	Formate dehydrogenase	C1-metabolism	0.0417	5.2	1.3E-05	3.3	1.1E-02	-1.9	1.2E-03
Solyc11g066430.1.1	Histone H2B.2	DNA.synthesis/chromatin structure.histone	0.0417	2.1	9.9E-04	1.4	ns	-0.7	2.9E-03
Solyc11g044840.1.1	Uncharacterized protein	amino acid metabolism.synthesis.aromatic aa.phenylalanine and tyrosine	-0.0448	-1.7	1.2E-04	0.3	ns	2.1	6.1E-04
Solyc03g117850.2.1	Uncharacterized protein	PS.calvin cycle.rubisco interacting	-0.0445	-3.8	4.0E-04	0.3	ns	4.1	4.0E-04
Solyc10g008980.2.1	Uncharacterized protein	transport.metabolite transporters at the envelope membrane	-0.0441	-1.8	1.6E-03	0.7	ns	2.5	7.0E-04
Solyc07g066310.2.1	Photosystem II 10 kDa polypeptide, chloroplastic	PS.lightreaction.photosystem II.PSII polypeptide subunits	-0.0441	-2.4	8.2E-04	0.7	ns	3.1	3.7E-04
Solyc04g011510.2.1	Triosephosphate isomerase	PS.calvin cycle.TPI	-0.0441	-0.6	6.1E-05	0.7	ns	1.3	3.4E-04
Solyc04g007790.2.1	Uncharacterized protein	stress.abiotic.unspecified	-0.044	-2.4	1.9E-04	0	ns	2.4	1.3E-03
Solyc12g056830.1.1	Uncharacterized protein	PS.lightreaction.ATP synthase.delta chain	-0.044	-1.4	1.0E-03	0.5	ns	2	1.5E-03
Solyc06g060340.2.1	Photosystem II 22 kDa protein, chloroplastic	PS.lightreaction.photosystem II.PSII polypeptide subunits	-0.0439	-1.7	1.3E-03	0.7	ns	2.5	6.3E-04
Solyc07g054820.2.1	Uncharacterized protein	not assigned.unknown	-0.0439	-1	7.4E-06	0.9	ns	1.9	2.2E-06
Solyc07g054820.2.1	Uncharacterized protein	not assigned.unknown	-0.0439	-1	7.4E-06	0.9	ns	1.9	2.2E-06

(cont. on next page)

Table 1.2. (cont.)

ID	Description	MAPMAN Category	PC1 Loading Score	homo/MM_fold	homo/MM_Pval	hemi/MM_fold	hemi/MM_Pval	hemi/homo_fold	hemi/homo_Pval
Solyc07g041920.2.1	Uncharacterized protein	protein.degradation.cysteine protease	-0.0438	-4.6	5.9E-05	-0.2	ns	4.3	2.6E-04
Solyc01g007530.2.1	Cytochrome b6	PS.lightreaction.cytochrome b6/f.cytochrome b6 (CYB6)	-0.0438	-3.2	1.5E-04	0.7	ns	3.8	3.4E-05
Solyc07g066610.2.1	Phosphoglycerate kinase	PS.calvin cycle.phosphoglycerate kinase	-0.0438	-0.5	5.6E-05	0.7	ns	1.2	4.1E-04
Solyc10g044520.1.1	Ferredoxin-1, chloroplastic	PS.lightreaction.other electron carrier (ox/red).ferredoxin	-0.0435	-0.9	2.3E-03	0.6	ns	1.5	4.1E-03
Solyc08g007040.2.1	Uncharacterized protein	PS.photorespiration.glycine cleavage.H protein	-0.0435	-1.2	5.1E-04	0.5	ns	1.6	2.2E-03
Solyc01g098640.2.1	Uncharacterized protein	not assigned.unknown	-0.0435	-1.6	2.7E-03	0.8	ns	2.3	1.3E-03
Solyc04g082250.2.1	FtsH-like protein	protein.degradation.metalloprotease	-0.0435	-0.3	6.3E-04	0.8	ns	1.1	1.9E-03
Solyc08g076290.2.1	Uncharacterized protein	not assigned.unknown	-0.0434	-2	4.2E-05	0.5	ns	2.6	3.4E-05
Solyc06g063370.2.1	Uncharacterized protein	PS.lightreaction.photosystem II.LHC-II	-0.0433	-0.6	1.5E-03	0.8	ns	1.4	1.3E-03
Solyc12g005630.1.1	Cytochrome b6-f complex iron-sulfur subunit	PS.lightreaction.cytochrome b6/f.iron sulfur subunit	-0.0433	-1.8	2.4E-03	0.4	ns	2.2	3.4E-03
Solyc02g077860.1.1	Uncharacterized protein	PS.calvin cycle.rubisco large subunit	-0.0431	-1.9	1.3E-03	0.3	ns	2.3	2.6E-03
Solyc10g011770.2.1	Uncharacterized protein	protein.degradation	-0.043	-5.1	1.5E-06	1.1	ns	6.6	1.0E-07
Solyc09g005620.2.1	SlGRX1 protein	transport.calcium	-0.0429	-3.8	3.8E-03	1.2	ns	5.1	8.4E-04
Solyc03g063560.2.1	Uncharacterized protein	N-metabolism.ammonia metabolism.glutamate synthase	-0.0429	-0.2	1.2E-03	0.7	ns	0.9	1.6E-02
Solyc10g052740.1.1	Photosystem I P700 chlorophyll a apoprotein A1	-	-0.0429	-1.3	6.3E-03	0.9	ns	2.2	2.0E-03
Solyc10g044540.1.1	Uncharacterized protein	PS.lightreaction.ATP synthase.alpha subunit	-0.0428	-0.9	1.8E-05	0.6	ns	1.6	5.6E-05
Solyc02g086730.1.1	Uncharacterized protein	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.50S subunit.L12	-0.0428	-0.9	6.9E-03	0.9	ns	1.8	3.1E-03
Solyc02g069460.2.1	Uncharacterized protein	PS.lightreaction.photosystem I.PSI polypeptide subunits	-0.0428	-0.7	3.2E-03	0.8	ns	1.5	2.7E-03

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Table 1.2. (cont.)

ID	Description	MAPMAN Category	PC1 Loading Score	homo/MM_fold	homo/MM_Pval	hemi/MM_fold	hemi/MM_Pval	hemi/homo_fold	hemi/homo_Pval
Solyc07g042440.2.1	Uncharacterized protein	redox.peroxiredoxin	-0.0426	-0.5	7.1E-04	0.8	ns	1.3	9.4E-04
Solyc08g068230.2.1	Uncharacterized protein	protein.postranslational modification	-0.0425	-0.6	3.4E-03	0.7	ns	1.3	8.0E-03
Solyc10g005050.2.1	Uncharacterized protein	PS.lightreaction.photosystem I.PSI polypeptide subunits	-0.0424	-5.1	3.3E-05	0.6	ns	5.6	1.3E-05

1.3.3.3. MAPMAN Annotation and Cluster Analysis of Proteomics Data

MAPMAN annotations were conducted for the acquired proteomics dataset for proteins with differential expression levels. Cluster analysis was conducted to visualize the expression patterns of identified proteins between different tested lines. When different test groups are mentioned we referto pairwise expression level comparisons between every pair of samples including each hemi and homozygous transgenic line versus wild type as well as each transgenic line versus all other transgenic individuals. As a result of the cluster analysis conducted in MAPMAN software, our proteomic data set was grouped into ten clusters based on expression patterns between different test groups (Figure 1.16).

Cluster 1 and 3 comprised of proteins which had slightes change in expression levels in transgenic lines compared to the nontransgenic line compared to other clusters. Other clusters consisted of proteins with more interesting expression patterns, with stronger changes in expression levels of transgenic lines compared to the nontransgenic line. Cluster 1 was comprised of 215 proteins with slight increase, decrease or no significant change in all group comparisons. Of these 215 proteins, 154, 105, 40 and 7 of them were significantly upregulated or downregulated in T6 homozygous, T19 homozygous, T6 hemizygous and T19 hemizygous individuals, respectively, compared to the nontransgenic line. Proteins in cluster 1 has a slight increase, decrease or no change in transgenic lines compared to the nontransgenic line thus the expression

profiles of the proteins were not very interesting and contained proteins from diverse functional categories (please see Appendix TableA.2). Cluster 3 was comprised of 127 proteins. In cluster 3, a slight decrease or no change was observed in T6 homozygous versus nontransgenic and T19 homozygous versus nontransgenic lines. Of the 127 proteins in cluster 3, 102, 99, 52 and 0 of them were significantly downregulated in T6 homozygous, T19 homozygous, T6 hemizygous and T19 hemizygous lines, respectively compared to the nontransgenic line (please see Appendix TableA.2). The MAPMAN categories of the most abundant groups in cluster 3 were as follows: 46 proteins in photosynthesis, 16 in protein metabolism, 6 in glycolysis, 5 in TCA, 5 in signaling, 5 in amino acid metabolism, 5 in RNA metabolism, 4 in transport and 4 in redox. The repressed proteins in cluster 3 were mostly in homozygous lines and mainly belonged to anabolic processes such as as photosynthesis, TCA, protein synthesis and amino acid biosynthesis.

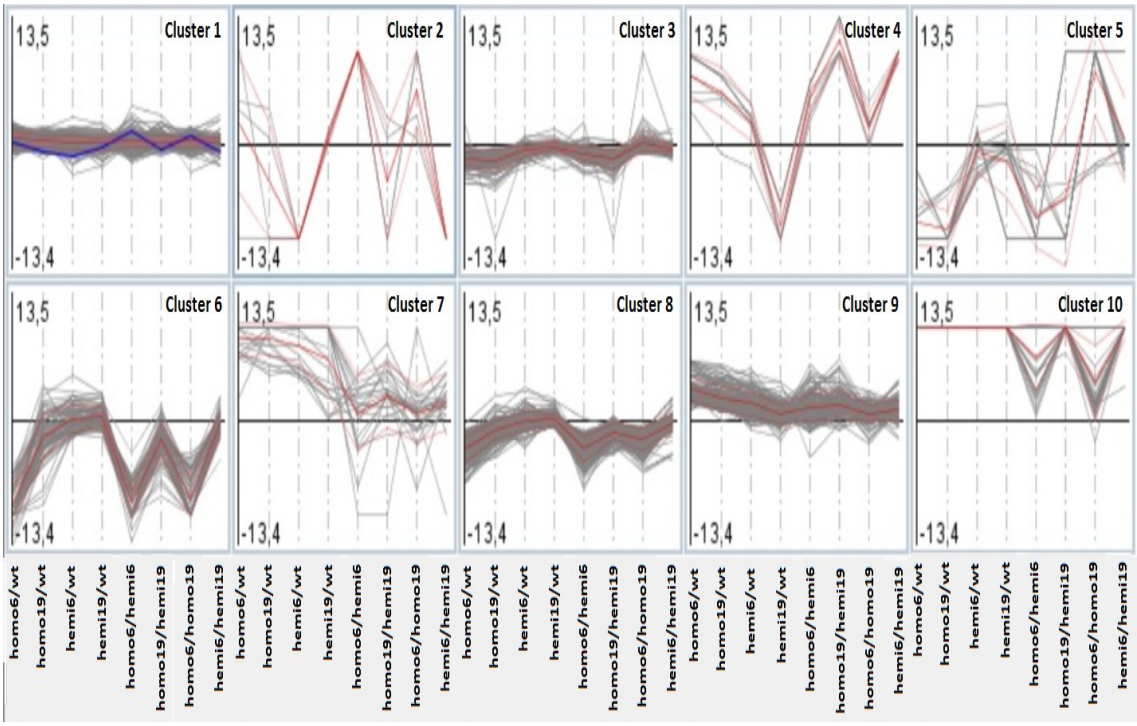

Figure 1.16. MAPMAN cluster analysis results for expression patterns of proteins in different experimental groups (comparisons are given on x-axis).

Clusters 10, 4, 7, 9 and 2 were composed of proteins which had increased levels in at least one homozygous line compared to the nontransgenic line. Cluster 10 contained 33 proteins most of which were only detected in homozygous and hemizygous lines and not detected in the nontransgenic line. The proteins in cluster 10

were very strongly inducedby CKs. Of these 33 proteins 33, 15, 6 and 0 of them were upregulated in T6 homozygous, T19 homozygous, T6 hemizygous and T19 hemizygous lines compared to the nontransgenic line, respectively (please see Appendix TableA.2). The MAPMAN categories of the most abundant groups in this cluster were protein metabolism with 9 proteins, followed by RNA metabolism with 3 proteins, TCA with 3 proteins, photosynthesis light reactions with 2 proteins, signalling with 2 proteins, amino acid synthesis with 2 proteins and abiotic stress with 2 proteins. Similar to cluster 10, cluster 7 contained proteins with an expression pattern exhibiting increased expression in both homozygous and hemizygous lines compared to the nontransgenic line. Cluster 4 consisted of 8 proteins, which were strongly upregulated only in both homozygous lines compared to the nontransgenic line. 8 and 6 proteins were upregulated in the T6 and T19 homozygous lines compared to the nontransgenic line, respectively (please see Appendix TableA.2). MAPMAN categories in the cluster were diverse with functions including fermentation, lipid metabolism, co-factor and vitamin metabolism, nucleotide metabolism, protein folding and cell death. Proteins with expression patterns similar to cluster 10 and 4 were observed in cluster 7. However, in cluster 7 a significant increase in expression levels in the T6 hemizygous line was detected with strong upregulationin T6 and T19 homozygous lines compared to the nontransgenic line. Cluster 7 was composed of proteins which are strongly induced by CKs. and was comprised of 23 proteins. Of these 23 proteins, 19, 17, 15 and 6 of them were significantly upregulated in T6 homozygous, T19 homozygous, T6 hemizygous, T19 hemizygous lines compared to the nontransgenic line, respectively (please see Appendix TableA.2). The MAPMAN categories of the most abundant groups in cluster 7 were stress with 4 proteins, mitochondrial electron transport with 2 proteins, cell wall with 2 proteins, lipid metabolism with 2 proteins, protein synthesis with 2 proteins, with the remaining proteins falling in diverse groups. Cluster 9 was composed of 143 proteins most of which were moderately upregulated in the T6 and T19 homozygous lines compared to the nontransgenic line, whereas few proteins were significantly upregulated in the T6 hemizygous and T19 homozygous lines compared to the nontrangenic line.Of these 143 proteins 139, 104, 47 and 9 of them were significantly upregulated in T6 homozygous, T19 homozygous, T6 hemizygous, T19 hemizygous lines compared to the nontransgenic line, respectively (please see Appendix TableA.2). The MAPMAN categories of the most abundant groups in cluster 9 were protein degradation with 16 proteins, stress with 10 proteins, protein synthesis with 9 proteins,

cell organization with 8 proteins, RNA with 7 proteins, lipid metabolism with 7 proteins, amino acid metabolism with 6 proteins, peroxidises with 5 proteins, glutathione S transferases with 4 proteins, glycolysis with 4 proteins, vesicular transport with 4 proteins, signalling with 4 proteins, cell cycle with 3 proteins, protein posttranslational modification with 3 proteins, transport with 3 proteins, photosynthesis with 3 proteins. Catabolism and stress related proteins were heavily represented in cluster 9, which were induced by high CK levels in T6 and T19 homozygous lines as compared to the nontransgenic line. Cluster 2 contained 4 proteins. Three of these proteins were upregulated in the T6 homozygous line, whereas one protein was downregulated in the T6 and T19 homozygous lines compared to the nontransgenic line (please see Appendix TableA.2). Cluster 2 was composed of proteins with MAPMAN categories including homone, amino acid and protein metabolism.

Clusters 5, 6 and 8 were composed of proteins which were downregulated in at least one homozygous line compared to the nontransgenic line. Cluster 5 contained proteins which were strongly repressed in the T6 and T19 homozygous lines, whereas just a few proteins were repressed in the T6 hemizygous line compared to the nontransgenic line. Cluster 5 was composed of 14 proteins. Of these 14 proteins, 10, 10, 3 and 0 of them were significantly downregulated in T6 homozygous, T19 homozygous, T6 hemizygous, and T19 hemizygous lines compared to the nontransgenic line, respectively (please see Appendix TableA.2). The MAPMAN categories of the most abundant groups in cluster 5 were protein metabolism with 6 proteins and signalling with 3 proteins. Cluster 6 was composed of proteins which were strongly repressed in the T6 homozygous line, whereas a smaller number of proteins were repressed in the T19 homozygous line and just a few proteins were repressed in the T6 and T19 hemizygous lines compared to the nontransgenic line. Of the 77 proteins in this cluster, 69, 33, 4 and 3 of them were significantly downregulated in T6 homozygous, T19 homozygous, T6 hemizygous, T19 hemizygous lines compared to the nontransgenic line, respectively (please see Appendix TableA.2). The most frequent MAPMAN categories in cluster 6 were protein synthesis with 8 proteins, protein targeting with 6 proteins, photosynthesis with 6 proteins, protein folding with 5 proteins, protein degradation with 5 proteins, signalling with 5 proteins, RNA with 3 proteins, hormone metabolism with 3 proteins, glutathione S-transferase with 2 proteins and protease inhibitor with 2 proteins. Cluster 8 was composed of proteins which were moderately repressed in the T6 homozygous line, whereas a smaller number of proteins were

moderately repressed in the T19 homozygous line and a few proteins were repressed in the T6 and T19 hemizygous lines compared to the nontransgenic line. Cluster 8 was composed of 157 proteins. Of these 157 proteins, 140, 57, 11 and 2 of them were significantly downregulated in T6 homozygous, T19 homozygous, T6 hemizygous, and T19 hemizygous lines compared to the nontransgenic line, (please see Appendix TableA.2). The MAPMAN categories of the most abundant groups in cluster 8 were photosynthesis with 31 proteins, protein synthesis with 20 proteins, signalling with 10 proteins, protein degradation with 9 proteins, transport with 7 proteins, protein posttranslation with 5 proteins, hormone metabolism with 5 proteins, secondary metabolism with 4 proteins, RNA with 4 proteins, glycolysis with 4 proteins, amino acid synthesis with 3 proteins and mitochondrial electron transposrt with 3 proteins. Clusters 5, 6 and 8 were composed of proteins that were heavily repressed in homozygous lines especially in the T6 homozygous line and these proteins were mainly related to anabolic processes such as photosynthesis, proteins synthesis, amino acid synthesis and secondary metabolism, which could be a sign of metabolic stress in the T6 homozygous line.

1.4. Discussion

Two *SARK::IPT* transgenic tomato lines with single insertions were studied under both control conditions. We observed phenotypic changes which were more severe in some transgenic plants. We determined the zygosity levels of the transgenic plants and identified that plants with more severe changes were homozygous for the *IPT* gene. The phenotypic changes were necrosis on the edges of newly growing leaves and complete loss of the apex and stunting in severely affected plants. Some plants also had thickening of the vascular tissue in newly growing leaves, thicker leaf tissue and formation of adventitious shoots on petioles. We hypothesized that these symptoms could be related to over-production of cytokinins, especially in homozygous plants. In the literature it was shown that over-production of cytokinins was related to similar symptoms including new leaf necrosis, stunting, adventitious shoot formationon petioles and thickened vascular tissue in tobacco plants and increased stress damage (Faiss et al.,

1997) and cell death in plant suspension cultures (Kunikowska et al., 2013). A reduction in total fruit yield was observed in the transgenic plants despite increased leaf biomass and leaf water content in both homozygous and hemizygous transgenic plants. We quantified the mRNA expression levels of the *IPT* gene in transgenic plants grown in control conditions in mature leaf, young leaf and root tissues. We observed higher IPT expression levels in mature leaves in both lines compared to young leaves and roots in agreement with the previous studies carried out in *SARK::IPT* plants (Rivero et al., 2007; Delatorre et al., 2012).We did not observe a significant increase in *IPT* expression levels in homozygous lines as compared to the hemizygotes, which could be related to the higher stress and senescence status of the homozygous plants. Leaves of the transgenic plants were greener than nontransgenic plants and we did not observe leaf yellowing even in the oldest leaves of the transgenic plants, indicating delayed senescence of leaf tissue.

We carried out proteomic analysis in the mature leaves of two transgenic lines from both homozygous and hemizygous plants and the nontransgenic line in control conditions to understand the CK action mechanism in leaves with a special focus on understanding the delayed leaf senescence mechanisms. We carried out LC-MS/MS analysis of the leaf total proteome with a shot-gun proteomics approach and found that 912 proteins were differentially abundant in the analysed lines. As result of the MAPMAN annotations and MAPMAN cluster analysis, we obtained different groups of proteins which could have roles in the regulation of plant metabolism in response to increased levels of CK. In the following sections, interesting categories of proteins and their potential roles in the high CK transgenic lines are discussed.

1.4.1. Central Carbon Metabolism

Increased CK levels cause a delay in leaf senescence which is accompanied by changes in primary metabolism. The delayed leaf senescence phenotype caused by increased CK levels was demonstrated to be related to an altered source/sink relationship (Lara et al., 2004; Peleg et al., 2011). Plants with increased CK levels are more inclined to act as a sink and use the photosynthetic assimilates in the leaf tissues

with high CK content (Lara et al., 2004). As sucrose is the transport form of the photosynthetic carbon assimilates, cell wall invertases (INV2) are one o f the major regulators controlling source/sink relationship by controlling apoplastic phloem unloading (Roitsch et al., 2003). The CK mediated delayed leaf senescence phenotype was associated with increased cell wall invertase levels, and overexpression of *cell wall invertase* caused an ectopic delay of senescence (Lara et al., 2004). Soluble vacuolar invertases are another sucrose degrading enzyme with a significant role in sink tissues by controlling the storage of sugars, osmoregulation and cell expansion (Slugina et al., 2017). In our study cell wall invertase levels were strongly increased in both homozygous lines and T6 hemizygous line compared to nontransgenic line, however the increase in the T6 hemizygous line was statistically non-significant. A gradual increase was observed in cell wall invertase levels which could be correlated with the CK levels. In our study we also detected that vacuolar invertase had increased levels in both homozygous and hemizygous lines compared to the nontransgenic line, but that the increase in the T19 hemizygous line was not statistically significant. Increased levels of both cell wall invertase and vaculolar invertase are an indicator that the mature leaves of the transgenic plants act as a sink tissue and do not load their photosynthetic assimilates into phloem for transport into nonphotosynthetic and young photosynthetic tissue. Increased levels of vacuolar invertase could be an indicator for storage of photosynthetic assimilates. The homozygous lines had very strong overexpression of both cell wall and vacuolar invertase compared to hemizygous lines and the highest overexpression levels were observed in the T6 homozygous line, which could cause a stronger sink behavior in these homozygous lines. Indeed, the young apex tissue of homozygous lines died after flowering, which could be caused by starvation of the young tissue because the mature CK overexpressing leaves acted as a strong sink. Thus, the mature leaves used the photosynthetic assimilates and even assimilated more from phloem transport fluid, thereby preventing its use by the apex. Phloem loading is required for transport of photosynthetic assimilated from source mesophyll tissue via specific transporters localized in cell membranes of mesophyll cells into the companion cells and sieve elements (Turgeon et al., 2010). So phloem loading is another aspect for control of source/sink relationships. SUC2 (sucrose-proton symporter 2) is the major transporter for loading sucrose into phloem (Chandran et al., 2003). SUC2 was strongly repressed in homozygous lines compared to the nontransgenic line. Reduction of SUC2 levels in homozygous lines could be related to reduction of sucrose loading into phloem

from the mature leaf tissue which has high CK levels. Decreased SUC2 levels coul be a sign for a strong sink phenotype in mature leaves of homozygous transgenic lines, eventhough mature photosynthetic leaves act as source in normal plants.

PII protein is another important regulator of carbon and energy status. PII protein is an integrator of energy levels and carbon metabolism via interacting with some metabolic enzymes such as acelyl-coA carboxylase and *N*-acetyl-L-glutamate kinase. Thus this protein controls the activity of carbon and ATP consuming enzymes in plastids (Chellamuth et al., 2013). Increased levels of PII protein caused by the WRINKLED1 transcription factor induced glycolytic and fatty acid (FA) biosynthetic genes (Baud et al., 2010). In our study PII protein was upregulated in homozygous lines compared to the nontrangenic line. PII could be related to induction of glycolysis in homozygous lines. In our study we also observe increased levels of some (FA) biosynthetic enzymes. Two pyruvate kinase isozymes having roles in FA elongation were upregulated in both homozygous and hemizygous lines compared to the nontrasngenic line. Two more enzymes with roles in lipid elongationwere upregulated in both homozygous lines compared to nontransgenic. Another lipid synthesis elongation related was strongly upregulated in both hemizygous lines compared to the nontrasngenic line. Upregulation of the abovementioned fatty acid biosynthetic genes could be induced by PII protein, which was previously demonstrated to induce fatty acid biosynthetic enzymes. In our study we observed increases in four glycolysis related genes in at least one of the homozygous lines compared to the nontransgenic line. In contrast we observed a reduction in eight glycolytic enzymes in at least one homozygous line compared to the nontransgenic line. Reduction in glycolytic enzymes was mostly detected in homozygous lines which could be associated with increased stress levels. ACX (acyl-CoA oxidase 3) is a key enzyme having a role in the β-oxidation pathway for fatty acid degradation (Graham and Eastmond, 2002). Under carbohydrate starvation conditions, ACX expression levels increased in Arabidopsis (Contento and Bassham, 2010). Moreover, an ACX3 ortholog in tea plant was also reported to catalyze a step in the JA biosynthetic pathway (Chen et al., 2019). In our study, this protein was upregulated in T6 homozygous compared to the nontransgenic line which is a sign of increased stress inflicted by high CK levels.

CKs are one of the major regulators of leaf development and photosynthesis, which is the most distinctive process carried out in leaf tissue (Höning et al., 2018). CKs delay leaf senescence mainly based on their effect on the photosynthetic machinery

(Rivero et al., 2010). As expected CKs also have a role in chloroplast development and function (Cortleven and Schmülling, 2015). In previous proteomics studies, the majority of differentially regulated proteins were chloroplastic proteins (Cerny et al., 2013). In our study, 12.7% of differentially regulated proteins in the transgenic lines compared to the nontransgenic line were related to photosynthesis. Interestingly, just nineof the 95 (9.5%) differentially regulated photosynthetic proteins were upregulated, 86 proteins (90.5%) were downregulated. Most (55.8%) of the photosynthetic proteins with significantly reduced abundance were observed in at least one of the homozygous lines. For 33.7% of the differentially abundant photosynthetic proteins, reductions in at least one homozygous line and the T6 hemizygous line were observed compared to the nontransgenic line. For T19 hemizygous line no photosynthetic protein was observed to have reduced levels compared to the nontransgenic line in our study. The reduction in photosynthetic proteins in homozygous lines could be an indicator of metabolic stress induced by excessive CK levels in the plants. It has long been known that photosynthesis is inhibited by stress conditions including biotic and abiotic factors (Ashraf and Harri, 2013). Downregulation of photosynthetic genes especially the components of photosystem II was also reported in Arabidopsis plants with CK over-production under salt stress (Wang et al., 2015). In our study, the PSI components PsbP and PsaC and the PSII component PPD5 were strongly upregulated in both homozygous lines and the T6 hemizygous line compared to the nontransgenic line. PsbP protein has a significant role in PSI assembly (Liu et al., 2012).

PsaC is a component of PSI and has a role in transfer of electrons to ferrodoxin (Yu et al., 1995). CKs could be direct regulators of photosynthetic PsbP, PsaC and PPD5 proteins as they were strongly upregulated in transgenic lines eventhough other photosynthetic proteisn were downregulated in homozygous transgenic line compared to the nontransgenic. cpFBPaseII, FBA1, FBA8, FBA6 and CFBP1 are components of the Calvin cycle and were upregulated in the T6 homozygous line compared to the nontransgenic line. Arabidopsis orthologs of FBA6 and CFBP1 were shown to be regulated by CKs in a proteomics study (Cerny et al., 2013). FBA8 and FBA6 were identified to be induced by stress in Arabidopsis (Lu et al., 2012). Induction of the abovementioned Calvin cycle proteins could be related to stress induced by excessive CK levels in T6 homozygous lines.

Respiration is the process in which ATP is produced from NADPH and $FADH_2$ which are produced by the controlled oxidation of reduced carbohydrates through

glycolysis and from the breakdown products of glycolysis in tricarboxylic acid cycle (TCA) (Sweetlove et al., 2007). Crosstalk between photosynthesis, metabolite assimilation and catabolism has great importance for adjustment of plant metabolism during diurnal process, development, adaptation to environment (Sweetlove et al., 2007). Adjustment of energy status is of great importance in cells, if not done properly could cause oxidative damage with destructive effects over different cellular process (Møller et al., 2001). The tricarboxylic acid (TCA) cycleis a part of the respiratory metabolism for generation of NADH/$FADH_2$ and metabolic intermediates (Zhang and Fernie, 2018). Moreover, the TCA cycle interacts with and regulates photorespiration, photosynthesis, nitrogen metabolism and redox regulation (Araújoet al., 2011). In previous studies, malate dehydrogenase, aconitase, fumarase, succinate dehydrogenase and 2-oxoglutarate dehydrogenase were identified to control the TCA pathway and, as result, the flux of metabolites into the abovementioned associated pathways (Araújo et al., 2011). In our study, we identified that 20 genes with roles in the respiratory TCA cycle were differentially abundant in at least one of the transgenic lines compared to the nontransgenic line. Fourteen of these TCA related proteins wereupregulated in at least one transgenic line compared to the nontransgenic line. These proteins included subunits of pyruvate dehydrogenase complex, isocitrate dehydrogenase, aconitate hydratase, succinyl-CoA ligase, malate dehydrogenase, 2-oxoacid dehydrogenase, malate oxidoreductase and citrate synthase. In contrast, six of the TCA related proteins were downregulated in at least one transgenic line compared to the nontransgenic line including subunits of pyruvate dehydrogenase complex, NADP-malic enzyme 3, carbonic anhydrase and isopropyl malate isomerase. Mitochondrial dihydrolipoyl dehydrogenase (mtLPD) is a subunit of pyruvate dehydrogenase complex (PDHC), 2-oxoglutarate dehydrogenase complex (ODHC, 2-oxoacid dehydrogenase complex (BCDHC) and glycine decarboxylase complex (GDC). The majority of mtLPD takes part in the GDC in photosynthetic tissue and has a role in flux through photorespiratory glycine to serine conversion (Timm et al., 2015). Activation of photorespiration is a protective mechanism to prevent photo-oxidative damage under stress conditions (Raghavendra and Padmasre, 2003). Downregulation of both mtLPD and GDC could be associated with a reduction in photorespiratory flux in both homozygous lines, which could cause a reduction in photooxidative damage conferred by photorespiration, thereby resulting a more severe inhibition and damage in photosynthetic machinery. The lack of the protective effect of photorespiration could be associated with the

decreased levels of photosynthetic proteins in homozygous lines in our study. NADP-ME2 (NAD-dependent malic enzyme 2) is related with generation of reducing power in the cytosol for anabolic processes, possibly assisting the oxidative pentose phosphate pathway (Wheeler et al., 2005). NAD-ME overexpression also conferred abiotic stress tolerance in wheat (Fu et al., 2011). In our study NAD-ME1 protein levels were increased in in both homozygous lines compared to the nontrangenic line. Similarly NAD-ME2 protein levels were increased in both homozygous and hemizygous lines compared to the nontrangenic line. NAD-ME2 could compensate for the decreased generation of reducing equivalents due to the inhibition of photosynthesis in homozygous lines. In our study we observed strong induction of citrate synthase in the T6 homozygous line compared to the nontransgenic line. Citrate sythase converts malate to citrate, when noncyclic TC flux mode is induced citrate synhtase and malic enzyme levels were identified to be increased and produced citrate is transported to cytosol (Sweetlove et al., 2010). Increased levels of citrate synthase and malic enzyme could be associated with an altered mode of TCA cycle in homozygous plants caused by metabolic stress induced by high CK levels. In our study prohibtin 2 (PHB2) was identified to be upregulated in homozygous lines compared to the nontransgenic line. PHBs are proteins locating in mitachondira and stabilize different protein complexes in the respiratory system (Piechota et al., 2015). In Arabidopsis PHB2 was identified to interact with and stabilize enzyme complexes containing lipoic acid cofactor including 2-oxoacid dehydrogenase, pyruvate dehydrogenase and glycine decarboxylase (Piechota et al., 2015). In our study we both observe increase in 2-oxoacid dehydrogenase and some subunits of pyruvate dehydrogenase in homozygous lines compared to the nontransgenic line. Increased PHB2 could be associated with the metabolic stress inflicted by high CK levels in homozygous lines to stabilize components of respiratory system. In our study we observed reduction in levels of carbonic anhydrase (CA) β1 and β4 in homozygous transgenic lines compared to the nontransgenic line. CAs are enzymes having role in concentrating CO_2 for an efficient photosynthetic activity (Moroney et al., 2011). CA β1 and β4 were identified to have role in CO_2 regulated stomatal movement (Hu et al., 2011). Increased bicarbonate levels in guard cells caused by CA β1 and β4 activity was identified to cause closure of stomata (Xue et al., 2011). Reduced levels CA β1 and β4 could cause reduced CO2 levels and reduced

photosynthesis levels in homozygous lines and could be related to stomatal opening in homozygous lines.

Electron transport chain (ETC) is the final process for respiratory ATP production in mitochondria and it is strictly regulated by other metabolic processes as photosynthesis and carbohydrate catabolic processes (Schertl and Braun, 2014). Electron transport chain consists of five respiratory complexes, from which electrons flow through Complex I (NADH dehydrogenase) then Complex II (succinate dehydrogenase) through ubiquinon Complex III (cytochrome c reductase) to cytochrome and finally to Complex IV (cytochrome c oxidase) where water is produced. ATP sythase (Complex V) utilize the proton gradient produced during the transport of electrons into water in ETC (Dudkina et al., 2006). In our study we identified that four subunits of mitochondrial ATP synthase were upregulated in at least one transgenic line, whereas three subunits were downregulated in T6 homozygous line compared to the nontransgenic line. Changes in protein levels of mitochondrial ATP synthase subunits could be related to regulation of ATP synthesis levels in mitochondria. But the reduction in the socalled levels of ATP synthase subunits was just observed in T6 homozygous line which could be an indicator of increased metabolic stress. ATP synthase activity is also known to be affected by adenylate kinase (ADK) activity (Igamberdiev and Kleczkowski, 2015). Moreover in our study components of ETC Complex III and IV, cytochrome c oxidase subunit 6b, apocytochrome c_1 and cytochrome c oxidase subunit 2 were identified to be differentially abundant at least one transgenic line compared to the nontrangenic. Levels of cytochrome c oxidase subunit 6b, apocytochrome c_1 were identified to be increased in both homozygous lines; however cytochrome c oxidase subunit 2 levels were identified to be reduced in T6 homoygous. Reduction in cytochrome c oxidase subunit 2 levels could be associated with increased metabolic stress levels in T6 homozygous line caused by high CK levels. Increased levels of cytochrome c oxidase subunit 6b, apocytochrome c_1 in homozygous lines could be caused by regulation of ATP biosynthesis by increased CK levels.

Adenylate kinase I (ADK1) is an enzyme catalyzing reversible conversion of AMP to ADP by transfer of a phosphoryl group from ATP. ADK1 has a significant role in cellular energy status by contributing to the control of adenylate energy charge (AEC) (Lange et al., 2008). AEC depends on the ATP/ADP ratio which has a role in fine tuning respiration and photosynthesis reactions (Igamberdiev and Kleczkowski, 2006). Under re-drying conditions of pea seeds, ATP metabolic demand was supplied by

ADK1 activity, when oxidative phosphorylation was no longer effective (Raveneau et al., 2017). In our study ADK1 was strongly upregulated in both homozygous and hemizygous lines compared to the nontransgenic line. Strong induction of ADK1 in all transgenic lines could be associated with regulation of energy metabolism and availability of energetic intermediates in CK over-producing lines.

1.4.2. Vascular Development and Cell Wall Structure

CKs are the major regulator of cambial growth and increased CK levels cause increasednumber of cells in both phloem and xylem (Matsumoto-Kitano et al., 2008). SEOR1 (sieve element occluding) are filamentous proteins having a role in formation of the ultra-structure of phloem tubes (Anstead et al., 2012). Callose is also an important constituent in phloem tubules controlling its permeability to phloem sap liquids controlled by Ca^{2+}signaling (De Storme and Geelen, 2014). 1,3 glucan synthases and β-1,3 glucanases controls the callose deposition in phloem tissue and plasmodesmata via synthesis and degradation (Zavaliev et al., 2011). In our studyfour SEOR1 paralogs were identified to have increased levels in both homozygous lines and T6 hemizygous compared to nontransgenic. In our study we identified two beta-1,3-glucanase isoforms. One of the beta-1,3-glucanase was downregulated in T6 homozygous and hemizygous line; and other was identified to have increase levels in T6 homozygous line. In our transgenic lines we observed larger venations in leaf tissues and also thicher stem tissue. CKs could directly regulate SEOR proteins which could contribute vasculature changes induced by CKs.

EXPs (expansins) are cell wall proteins having a role in cell wall loosening for facilitating cell enlargement, cell proliferation and senescence in a plant hormone responsive manner (Choe and Cosgrove, 2010). Overepression of an expansin protein caused bigger cells in transgenic plants (Cho and Cosgrove, 2000). CKs are known to increase proliferation rates in plant cells and CK feeding of cultured cells causes increased expansin b levels (Downes and Crowell, 1998). In our study we identified an expansin protein with increased levels in both homozygous lines compared to transgenic

line. Expansin could be a CK regulated protein as it is induced all transgenic lines and it could have role in cell wall structure and cell size determination in transgenic lines.

Annexins (ANNAT) are Ca^{2+} binding proteins, localizing to plasma membrane in high Ca^{2+} levels act in signal transduction and have a role in Golgi mediated secretion of cell wall and membrane materials (Cantero et al., 2006). Annexin proteins were also reported to have a role in abiotic and biotic stress response (Laohavisit and Davies, 2011). In addition, annexins were identified to localize in phloem and hypothesized to have a role in phloem transport of sugars into roots (Wang et al., 2018). In our study three ANNAT paralogs were upregulated in all transgenic lines compared to nontransgenic line. ANNAT4 and ANNAT1 seem to be positively regulated by increased CK levels. In a study conducted in tomato, CK-responding putative cis regulatory elements were detected for tomato *ANNAT* genes (Lu et al., 2012) providing a mechanism for their altered expression in the transgenic plants.

During cell proliferation and growth, cell wall rigidity is altered and a complex array of changes in cell wall biochemistry drives those processes. Pectinesterases are important agents for cell wall loosening during the abovementioned cellular processes together with expansin proteins (Chebli and Geitmann, A., 2017). Other enzymes are also required for cell wall maintenance and required for cell wall biochemistry modification during different processes such as cell proliferation, cell expansion, senescence, fruit maturation, pathogen defence and abiotic stress tolerance.These enzymes include glycoside hydrolases, UDP-glucose dehydrogenase and UDP-arabinose mutase (Cosgrove, 2016). In our study four pectine esterase enzyme isozymes were differentially abundant in transgenic lines compared to nontransgenic line. A pectin esterase enzyme was upregulated in both homozygous and hemizygous lines compared to the nontransgenic line. Another pectin esterase enzyme was only induced in homozygous line compared to nontransgenic line. Whereas two pectin esterase isozymes were downregulated in both homozygous lines compared to the nontransgenic line. As CKs are hormones inducing cell proliferation and growth, cell wall biochemistry must be changed and different isozymes of pectin esterases could contribute to that process in different ways. Three cell wall modifying enzymes (UDP-glucose dehydrogenase, beta-glucosidase and GDP-D-mannose epimerase) were downregulated in both homozygous lines compared to the nontransgenic line. In addition a cell wall modifying enzyme (glycoside hydrolases) was upregulated in the T19 homozygous line compared to the nontransgenic line. In our study we also

identified other enzymes having role in cell wall biosynthesis and modification which are glucoside hydrolases. ARAF1 (Alpha-l-arabinofuranosidase/beta-d-xylosidase) is a glucoside hydrolase enzyme having role in cell wall modification in vasculature tissue in pholoem, xylem vessels and parenchyma cells surrounding vessels. Overexpression of ARAF1 was identified to cause changes in vascular tissue architecture (Montes et al., 2008). ARAF1 was identified to be downregulated in T6 homozygous line, whereas upregulated in T19 hemizygous compared to nontransgenic line. GM (mannosidase) is also a glucoside hydrolase family enzyme with a role in formation of complex N-glycans in Golgi, which contributes to glycoprotein synthesis and/or cell wall biosynthesis (Strasser et al., 2006). In our study a GM protein was induced in both homozygous and T6 hemizygous line, which could be a sign that it is a protein positively regulated by CK hormone. MSBP2 (membrane steroid-binding protein 2) is a structural component of ER. MSBP2 stabilizes lignin biosynthetic cytochrome P450 enzyme thus, indirectly affect lignin biosynthesis (Gou et al., 2018). In our study, MSBP2 was upregulated in all homozygous lines compared to the nontransgenic line. MSBP2 could have role in vascular tissue development.

The cytoskeleton has a significant role in cell shape determination during events such as cell proliferation, cell growth and elongation (Smith and Oppenheimer, 2005). Microtubule and microfilaments are of great importance for cell wall structure determination and they direct cell wall biosynthetic enzymes into plasmalemma (Wightman and Turner, 2008). It was demonstrated that increased CK levels causes over-representation of cytoskeleton related proteins in *Arabidopsis* (Cerný et al., 2014). In a transcriptomic expression study in response more than half of all cytoskeleton related genes were identified to be upregulated in reponse to CKs (Brenner et al., 2005). In our study six actin protein paralogs were upregulated in homozygous lines and for some paralogs also in hemizygous lines. Also we observed four profilin paralogs were upregulated in both homozygous lines and T6 hemizygous line compared to nontransgenic. In addition three tubulin paralogs were upregulated in both homozygous lines and hemizygous lines compared to the nontransgenic line. CAP1 is a nucleotide exchange factor required for actin polymerization events and has roles in cell elongation and division (Deeks et al., 2007). CAP1 was upregulated in the T6 homozygous line compared to nontransgenic line. Upregulation of cytoskeleton proteins in transgenic lines is a sign of their regulation by CKs and is related to the changes in cell shape or cell wall synthesis that occurred in CK overexpressing lines.

WPP is a protein with a role in mitotic activity and localized in the nuclear envelope (Brkljacic et al., 2009) and Golgi (Patel et al., 2005). In our study, WPP was strongly upregulated in homozygous transgenic lines compared to the nontransgenic line. WPP protein could have a role in cell proliferation and organization and could be regulated by CKs.

1.4.3. ROS Scavenging Mechanisms and Detoxification

Senescence induced increase in endogenous CK levels were reported to improve ROS scavenging system by both induction of antioxidant enzymes and production of non-enzymatic antioxidants (Rivero et al., 2007; Xu et al., 2016). But also opposing results were reported about deterioration of oxidative stress caused by endogenously increased CK levels associated with reduced tolerance against salinity stress (Wang et al., 2015). The reported opposing results could be related to the concentrations of endogenous CKs. Previously excessive CK levels were reported to inflict stress in plants and even to cause cell death (Carimi et al., 2003; Novák et al., 2013). Glutathione is one of the key antioxidant molecules and its conjugation to oxidized molecules reduces them via different enzymes or some enzymes use glutathione as to reduce metabolites as H_2O_2 without conjugation. Enzymatic reactions related to glutathione comprises of backbone for ROS scavenging mechanisms. Glutathione is used to reduce H_2O_2 metabolites via peroxidases including ascorbate peroxidase (APOX), peroxiredoxin (PRX), glutathione peroxidases (GPX) and glutathione-S-transferases (GSTs) (Kapoor et al., 2015). Oxidized glutathione produced as a result of activities of abovementioned reaction is reduced back to antioxidant form via glutathione-disulfide reductase (Bick et al., 2001). Thioredoxins help to protect proteins from oxidative stress, act as signalling molecules by changing the redox state of proteins and some can act as co-chaperones and some has role in oxidative stress tolerance (Balmer et al., 2004; Spoel and Loake, 2011; Prasad et al.,2010). In our study four ascorbate peroxidase isozymes were identified to be upregulated in at least one homozygous line compared to nontransgenic line. But an ascorbate peroxidase isozymes were down regulated in all homozygous and T6 hemizygous line compared to nontransgenic line,

which could be strong negative regulation by CKs. In our data set four GST (glutathione S-transferase) isozymes were upregulated at least one of the homozygous lines compared to nontransgenic. But two GST isozymes were downregulated in homozygous lines compared to nontransgenic line. In our study, three peroxiredoxin family proteins were detected and two of them were upregulated in homozygous lines compare to nontransgneic, whereas one isozyme was down regulated in homozygous line compared to nontransgenic line. Three catalase isozymes were significantly differentially regulated and two of them were upregulated in at least one of the homozygous line and one isozyme was downregulated in T6 hemizygous line compared to nontransgenic line. Two superoxide dismutase isozymes were identified to be upregulated in homozygous transgenic lines compared to nontransgenic line. ATGR1 (glutathione-disulfide reductase) was also upregulated in homozygous lines compared to nontransgenic line. A glutaredoxin was strongly upregulated in all homozygous and T6 hemizygous line compared to nontrasngenic line. In our study also three isozymes of thioredoxin family proteins were downregulated at least one of the homozygous lines compared to nontransgenic. In our study we also observed upregulation of seven peroxidase family proteins which both have role in oxidative stress related mechanisms and cell wall biosynthesis. As is discussed above, several antioxidant enzymes were differentially regulated in transgenic lines compared to nontransgenic in our study which can be related to CK dependent regulation of these enzymes.

NDPK (nucleoside diphosphate kinase) both have role in nucleotide metabolism and in signaling and stress-related pathways. NDPK2 was identified to have role in regulation of oxidative stress by interacting with MAPKs (Moon et al., 2003). *NDPK1* over-expression was identified to confer improved tolerance against exogenously applied H_2O_2 (Fukamatsu et al., 2003). *NDPK2* over-expression was also identified to confer improved tolerance to reactive oxygen species in Arabidopsis (Yang et al., 2003). Similarly *NDPK3* over-expression was identified to induce antioxidant enzymes APX, CAT, POX and oxidative stress response, acting as a positive regulator of stress response (Liu et al., 2015). In our study NDPK3 levels were reduced in both homozygous lines compared to nontransgenic line. Reduction of NDPK3 protein levels in homozygous lines could be sign of negative regulation by high CK levels and it could result in weakening of oxidative stress response in homozygous lines. NDPK2 levels were just reduced in T6 homozyous line compared to nontransgenic line, no significant

change was observed in other lines. In our study we also detected NDPK1 and it had reduced levels in T6 homozygous compared to nontransgenic.

Ferritins are iron storage proteins, having role in sequestration of iron. As free iron can induce formation of ROS via Fenton reactions, ferritin has role in abiotic stress response (Reyt et al., 2015). Overexpression of ferritin proteins was identified to confer abiotic stress tolerance via improving ROS scavenging (Zang et al, 2017). In our study, two ferritin paralogs were identified to have increased levels T6 homozygous and T6 hemizygous lines compared to nontransgenic.

FDH (formate dehydrogenase) is universal stress protein upregulated under abiotic and biotic stress conditions (Alekseeva et al., 2010). FDH detoxifies formate which is produced during metabolic events as photorespiration, gyoxylate decarboxylation and methanol metabolism (Li, et al., 2003). In our study FDH strongly upregulated in T6 homozygous and both hemizygous lines compared to nontransgenic. SFGH (S-formylglutathione hydrolase) is an enzyme having role in detoxification formaldehyde produced form metabolic processes (Kordic et al., 2002). Levels of formaldehyde is known to be increased under biotic and abiotic stress conditions and SFGH levels were reported to increased under these stress conditions (Sun et al.,2014). SFGH was identified to have increased levels in homozygous lines compared to nontransgenic lines. ALDHs (aldehyde dehydrogenases) are enzymes detoxifying aldehydes. Aldehydes are produced during metabolic processes as lipid peroxidation and their accumulation rates increase under stress conditions (Stiti et al., 2011). ALDHs are also known to be upregulated under stress conditions and their upregulation improves stress tolerance in different plant species (Stiti et al., 2011). In our study, two ALDH isozymes were upregulated in homozygous lines compared to nontransgenic line. GLXs (glyoxalases) are enzymes metabolizing toxic methylglyoxal byproduct of glycolysis, lipid peroxidation and oxidative degradation of glucose (Yadav et al., 2005a). Accumulation of methylglyoxal production is a byproduct oxidative stress and its levels increases under stress conditions (Yadav et al., 2005b). In our study GLX1 levels were identified to be increased in both homozygous lines and T6 hemizygous linecompared to nontransgenic. CYN (cyanase) is an enzyme having role in detoxification of cyanide produced during ethylene production (Johnson and Anderson, 1987). Its levels were identified to be increased under abiotic stress conditions (Qian et al., 2011). In our study CYN was upreglated in T6 homozygous line compared to nontransgenic.

In most of the suppressed proteins, we observed a pattern of down-regulation following a suppression pattern from mildest to strongest in T19 hemizygous, T6 hemizygous, T19 homozygous and T6 homozygousplants compared to nontransgenic line, respectively. It could be a sign that the proteins of interest are suppressed by the metabolic stress caused by excessive levels of CKs or these proteins are negatively regulated by a gradual increase in CK levels. This gradual downregulation pattern could be a result of the metabolic stress, which abolishes their expression. In our study the abovementioned expression pattern was observed for same ROS scavenging enzymes and redox regulator thioredoxins. In most of the upregulated proteins, we observed a pattern of upregulation following an increase pattern from mildest to strongest inT19 hemizygous, T6 hemizygous, T19 homozygous and T6 homozygous plants compared to nontransgenicline, respectively. It could be a sign that the proteins of interest are induced by the metabolic stress caused by excessive levels of CKs or these proteins are positively regulated by a gradual increase in CK levels. This gradual increase pattern was observed in detoxification proteins as CYN, FDH, GLX and ALDH which metabolizes toxic side products of primary and secondary metabolism. Some antioxidant enzymes displayed the gradual upregulation pattern as well.

1.4.4. ER Stress and Protein Folding

Endoplasmic reticulum (ER) is the site of protein synthesis, folding, assembly and export. ER quality control (ERQC) checks protein quality during all of these processes. During both abiotic and biotic stress conditions, levels of misfolded proteins increase and exceed the capacity of ERQC, causing accumulation of misfolded proteins which is called ER stress (Liu and Li, 2014). Long term and intense ER stress causes damage to the ER and other organelles and causes induction of cell death. Organisms induce a response against ER stress for refolding and degrading misfolded proteins which is called the unfolded protein response (Howell, 2013). During this response, the homeostasis in protein synthesis is restored by three major mechanisms: expression of chaperonin and foldases to increase protein folding; ER-associated degradation (ERAD) for removal of misfolded proteins; and attenuation of secretory protein synthesis to

prevent accumulation of more unfolded proteins (Wan and Jiang, 2016). Induction of ER stress activates the bZIP transcription factor which causes expression of the ER-resident chaperone BIP and HSP70 which take part in refolding of misfolded proteins (Braakman and Hebert, 2013). In our study, one BIP1 and three BIP2 paralogs had increased levels in both homozygous lines and the T6 hemizygous line compared to the nontransgenic line. In our study, nine HSP70 paralogs had significantly altered protein levels compared to the nontransgenic line, eight of these HSP70 paralogs had increased levels in both homozygous and hemizygous lines. However, one HSP70 paralog had decreased levels in the homozygous line compared to the nontransgenic line. HSP90.1 was upregulated in both homozygous lines and the T6 hemizygous line compared to the nontransgenic line. Calreticulin and calnexin proteins are also components of the ER protein folding machinery, which recognises glycoproteins (Liu and Li, 2014). CRT3 (Calreticulin 3) and calnexin 1 (CNX1) levels were increased in homozygous and hemizygous lines as compared to the nontransgenic line. BAG7 (BCL-2-associated athanogene 7) is a calmodulin binding protein with a co-chaperone activity and BAG proteins are known to control cytoprotective activities in development, biotic and abiotic stress processes (Doukhanina et al., 2006). BAG7 was identified to be involved in the unfolded protein response during ER stress as a cytoprotective chaperone (Williams et al., 2010). In our dataset, BAG7 levels were significantly increased in both T6 and T19 homozygous lines compared to the nontransgenic line. CCT8 (T complex protein 1 subunit theta) is a chaperonin protein with a role in protein folding especially acting as subunit of CCT protein folding machinery (TCP-1 ring complex), and also a role in trafficking of proteins through plasmodesmata (Xu et al., 2011; Willison, 2018). CTT7 (T-complex protein 1 subunit eta) and CCT6A (T-complex protein 1 subunit zeta 1) are also subunits of CCT protein folding machinery (Willison, 2018). CCT7 and CTT8 were strongly induced in both homozygous lines but no significant change was observed in hemizygous lines compared to the nontransgenic lines. CCT6A was also identified to have increased levels in both T6 and T19 homozygous lines compared to nontransgenic line, which was just statistically significant for T6 homozygous line. CCT6A and CCT7 were also induced by cadmium stress in Arabidopsis (Sarry et al., 2006), which could be a sign that CCT protein folding machinery has an important role in stress response mechanisms by alleviating the unfolded protein response in cells. CCT subunits could be upregulated in the homozygous lines in response to the unfolded protein response.

PDI proteins have a role in formation of disulfide bonds during protein folding in ER (Bulleid, 2012). Prolyl peptidyl cis–trans isomerases (PPIases) also have a role in protein folding via controlling conformation of proline residues in proteins. Cyclophlins (CYP) and FK-binding proteins (FKBP) are a subgroup of PPIase family proteins (Schiene-Fischer, 2015). Cyclophilin and FKBP proteins can have diverse roles via interaction with other proteins. For instance, FKBP12 (FK506-binding protein) is known to interact with a FIP37, a DNA binding protein having a role in cell cycle regulation and embryo development (Faure et al., 1998). Overexpression of alpine haircap moss *PaFKBP12* in Arabidopsis conferred abiotic stress tolerance and improved plant growth (Allavi et al., 2018).PDI-like protein had increased levels in the T6 homozygous line compared to the nontransgenic line. In our study, 7 PPIase family proteins had significantly changed levels. Two CYP 5 paralogs, 2 FKBP paralogs and 2 PPIase ROC3 paralogs had increased levels in the homozygous line compared to nontransgenic line. In contrast, a FKBP13 had reduced levels in homozygous lines compared to the nontransgenic line. ROF1 (rotamase FKBP 1) is a calmodulin binding protein, acting as a co-chaperone and having a role in termotolerance and osmotic stress tolerance with distinct mechanisms in Arabidopsis (Karali et al., 2012; Meiri et al., 2009). In our dataset, ROF1 protein levels were significantly increased in both T6 and T19 homozygous lines compared to the nontransgenic line.

Nascent polypeptide-associated complex (NAC) interacts with emerging polypeptides during translation progression to prevent them from bind other cytoplasmic factors, thereby acting as a chaperonin for newly growing polypeptides (Rospert et al., 2002). In mammalian and yeast, NAC was identified to have roles in shielding newly growing polypeptide during translation, transcription activation, and ER stress response (Preissler and Deuerling, 2012). In our study, a NAC subunit was upregulated in the T6 homozygous line compared to the nontransgenic line. Upregulation of NAC subunit in the T6 homozygous line could be related to ER stress for alleviation of unfolded protein stress.

Upregulation of chaperone proteins and other proteins with roles in protein folding such as PPIses could be caused by ER stress in the homozygous lines. If the unfolded protein response is not alleviated by expression of chaperonin, foldases and proteases, organelles can undergo autophagy and cells can undergo programmed cell death (Wan and Jiang, 2016). In the protease section, we discussed the role of proteases during senescence, stress response and cell death. In our dataset, we detected many

proteases from different families which had increased levels in homozygous lines and could have roles in alleviation of unfolded protein response and ERAD.

1.4.5. Protein Degradation

Plant proteases regulate turnover of proteins having significant roles during diverse biological processes including development, senescence, plant defense and programmed cell death (Van der Hoorn, 2008). Plant cysteine proteases are the most abundant class of proteases induced during senescence and are also involved in defense responses (Guo et al., 2004; Salguero-Linares et al., 2019). Under environmental or developmental stress and during senescence, protein degradation rate increases (Araújo et al., 2011). Cathepsin B was identified to be induced by endoplasmic reticulum (ER) stress and has a role in ER-stress induced cell death (Ge et al., 2016). In our study, we identified seven cathepsin paralogs which were upregulated or downregulated in either homozygous or hemizygous lines compared to nontransgenic lines. Three cathepsins paralogs were strongly induced in homozygous lines compared to the nontransgenicline. A cathepsin paralog was slightly induced in the T6 homozygous line compared to the nontransgenic line, whereas two cathepsin paralogs were strongly downregulated in homozygous lines compared to the nontransgenic line. One of the strongly downregulated proteins was SAG2 which is a protease associated with senescence and nutrient remobilization (Grbić, 2003). In previous studies, it was reported that increased CK levels delay stress induced senescence (Rivero et al., 2007).

Aspartic proteinases (APs) have diverse roles in plants such as degradation of storage proteins during germination, defense mechanisms against pathogens and during senescence (Mazorra-Manzano et al., 2010). An AP protein had increased levels in all homozygous lines and in the T6 hemizygous line compared to the nontransgenic line. OOP is a metalloprotease localized in mitochondria and chloroplast having a role in degradation of targeting peptides after localization in the target organelle and also in degradation of peptides produced during the complete protein degradation process as a quality control mechanism (Kmiec et al., 2013). In our study, OPP levels increased in both homozygous lines compared to the nontransgenic line. Clp protease complex is the

major factor controlling protein turnover in the chloroplast (Nishimura et al., 2016). As plastids are the site of fatty acid, amino acid, nucleotide, tetrapyrrole and isoprenoid biosynthesis the levels of biosynthetic enzymes are controlled by the Clp protease complex. Moreover this complex has a role in degradation of misfolded proteins (Rodriguez-Concepcion et al., 2018). In our study, two Clp protease subunits were upregulated in T6 and T19 homozygous lines compared to the nontransgenic line. Upregulation of Clp protease in homozygous lines could be a sign of increased client proteins, possibly defective proteins in the plastids. The substilase protease family is a member of serine peptidases which are generally targeted to cell walls and have diverse roles in growth, development and deference responses via control of protein turnover (Shaller et al., 2012). For instance, SDD1 has a role in stoma development (Van Groll et al., 2002) and ARA12 negatively regulates pectin methyl esterase activity during the late stage of seed development in *Arabidopsis* (Rautengarten et al., 2008). In our study we observed increased levels of 2 SDD1 paralogs compared to the nontransgenic line in the T6 homozygous line. In contrast, a reduction was observed in SBT1.9 levels in the T6 homozygous line compared to the nontransgenic one. LAPA (leucine aminopeptidase) is a protease with a role in wound response, acting downstream of the JA signaling pathway and conferring tolerance against insects in tomato (Fowler et al., 2009; Chen et al., 2005). In our study we detected two paraologs of LAPA which were upregulated in both homozygous lines compared to the nontransgenic line. AAA-ATPase chaperones are barrel shaped multimeric proteins that remodel target proteins from protein complexes using the energy from ATP hydrolysis in association with cofactors (Erzberger and Berger, 2006). CDC48 proteins are member of AAA-ATPases having diverse roles in different processes such as endoplasmic reticulum associated degradation (ERAD), chromatin and mitochondrial associated protein degradation and recruitment, which control different biological processes such as protein quality control and degradation, gene expression, DNA replication and repair and membrane fusion (Begue et al., 2017). Five paralogs of CDC48 had increased levels in both homozygous lines. CDC48 was also identified to have a role in cell division, expansion and differentiation (Park et al., 2008). Increased CDC48 levels could be associated with ER stress in homozygous lines.

The ubiquitin-proteosome system controls various aspects of plant growth and development via targeting and degrading proteins for control of protein turnover especially short-lived signaling proteins (Sadanandom et al., 2012). The 26S

proteoseome is composed of a 20S core protease carrying out the proteolytic function and a 19S regulatory particle recognizing, unfolding and submitting the target proteins into the 20S core (Voges et al., 1999). The 20S proteosome subunit PBA1 was also identified to have a role in programmed cell death caused by pathogens and ER-stress (Hatsugai et al., 2009; Cai et al., 2018). The 19S regulatory particle was found to be composed of a lid and base. The lid is composed of non-ATPase subunits (RPN3, RPN5–9, RPN11, RPN12, and RPN15) and the base is composed of six AAA+ ATPase subunits (RPT1–6) and four non-ATPase subunits (RPN1, RPN2, RPN10, and RPN13) carrying out denaturation of targeted proteins (Smith et al., 2007). Seven proteins which are 26S proteosome subunits were differentially abundant in our study. In addition, five differentially abundant proteins were components of the 20S core protease. All detected 20S core protease subunits were upregulated in both homozygous lines. Also a 20S proteosome subunit PBA1 was strongly induced in all homozygous lines and the T6 hemizygous line. Induction of PBA1 could be an indicator of ER stress in homozygous lines. We also identified six differentially abundant 19S regulatory particle subunits, four of which were significantly upregulated in both homozygous lines. An increase was also observed in hemizygous lines even though some of them were not statistically significant. We also observed that two 19S regulatory particle subunuits were downregulated in both homozygous lines compared to the nontransgenic line. Proteins that will be degraded in the proteosome pathway are targeted to that fate by ubiquitylation which is performed by ubiquitin ligases (E3 proteins) that are specific for their target proteins (Finley, 2009). Extra-proteosomal proteins are known to have roles in delivery of ubiquitylated proteins intermediated by specific binding to them. RAD23 (radiation sensitive 23) family proteins are known to shuttle proteins to the 26S proteosome and are also a component of the DNA excision repair factor complex (Farmer et al., 2010; Lahari et al., 2018). Moreover RAD23 proteins were found to be connected with the ERAD pathway and have roles in removal of incorrectly folded proteins (Raasi et al., 2007). In our study, two RAD23 paralogs were significantly upregulated in all homozygous lines and the T6 hemizygous line with a nonsignificant increase also observed in the T19 homozygous line. UEV1D-4 is anubiquitin E2 ligase catalyzing ubiquitination of specific proteins for regulation of them in a non-proteolytic manner, having a role in DNA damage tolerance (Wen et al., 2008). In our study UEV1D-4 was very strongly and significantly induced in both homozygous lines and T6 hemizygous lines compared to the nontransgenic line. FtsH protease is located in

thylakoid membranes and hs a role in maintenance of thylakoid membranes and recovery of photodamaged D1 from photosystem II (Kato and Sakamoto, 2018). Two subunits of FtsH had reduced levels in all homozygous lines compared to the nontransgenic line but no significant change was observed in hemizygous lines.

1.4.6. Plant Hormones and Signalling

Adenine phosphoribosyl transferase 1 (APT1) catalyzes a reaction in the conversion of adenine to AMP in the purine nucleotide salvage pathway (Allen et al., 2002). Moreover as CKs are adenine derivatives, APT1 has a role in the breakdown of free CK bases into nucleotides and has a pivotal role in breakdown of excessive CK (Zhang et al., 2013). APT1 loss of function mutants in *Arabidopsis* cause accumulation of CKs, induction of CK signaling associated gene expression and phenotypic changes (Zhang et al., 2013). In our study, APT1 was significantly upregulated in both T6 and T19 homozygous lines but no significant change was observed in the hemizygous line compared to the nontransgenic line. As APT1 was demonstrated to have a role in irreversible CK degradation, the homozygous transgenic lines which are hypothesized to high CK levels have increased levels of APT1, which could be associated with reduction of excessive CK levels. PUR4 (purine synthesis 4) is an enzyme with a role in de novo purine biosynthesis with a formylglycinamidine ribonucleotide synthase activity. De novo purine synthesis is of great importance for providing purine nucleotides for cell division and precursors for CKs, co-enzymes, ATP and GTP (Smith and Atkins, 2002). Moreover PUR4 was identified to be required for pollen development in *Arabidopsis* (Berthomé et al., 2008) and a cotton ortholog of this gene was identified to have a role in chlorophyll biosynthesis and chloroplast development. Increased PUR4 levels in homozygous lines could be associated with higher CK levels because high CK biosynthesis could require more precursors synthesized by PUR4. PURA (adenylosuccinate synthase) has a role in the purine biosynthetic pathway catalyzing the first step for synthesis of AMP from IMP (inosine-5'-monophospahte) (Prade et al., 2000). PURA levels were reduced insignificantly in the T19 homozygous line, however, the T6 homozygous line had significantly reduced levels compared to the

nontransgenic line. Reduction of PURA levels could be an attempt for limiting further CK biosynthesis by limiting the adenine precursors or could be a stress response to limit primary metabolic processes. PICKLE (PKL) is an ATP-dependent chromatin remodeler from the Mi-2/CHD3 subfamily with a role in regulation of gene expression by changing the conformation of the nucleosome and chromatin and controlling many developmental processes such as embryonic development, meristematic activity, seed germination and hypocotyl elongation (Ogas et al., 1999; Perruc et al., 2007; Aichinger et al., 2011). PKL was identified to control the transition from embryonic to vegetative development via suppressing the expression of genes from a certain chromosome region (Ogas et al., 1999; Sæther et al., 2007). PKL protein loss of function mutants exhibited a CK oversensitive phenotype, and was concluded to be a negative regulatory of CK response in *Arabidopsis* (Furuta et al., 2011). In our study PKL protein was very strongly reduced in the T6 homozygous line compared to the nontransgenic line. Reduction in the T6 homozygous line could be related to very increased levels of CKs and suppression of the CK response negative regulator PKL.

NCED4 (nine-cis-epoxycarotenoid dioxygenase 4) is a paralog of a ABA biosynthetic enzyme yet it is not clear if it has a role in ABA biosynthesis, however, it was demonstrated to have a role in carotenoid degradation in seed drying and leaf senescence processes in *Arabidopsis* (Gonzalez-Jorge et al., 2013). NCED4 was strongly downregulated in both homozygous lines compared to the nontransgenic line. *Arabidopsis* UDP-glucosyl transferase (UGT71B7) has a role in ABA inactivation via conjugation of glucose which causes formation of an inactive form of ABA-glucose ester which can be converted back to ABA by hydrolysis of the glucose moiety (Dong et al., 2014). In our study UGT71B7 was significantly down regulated in the T6 homozygous line compared to the nontransgenic line. SNRK2-6 is a serine/threonine kinase activated by ABA and acts drownstream of ABA receptors with a role in stomatal closure both in an ABA dependent and independent way (Kollist et al., 2014). SNRK2-6 was upregulated in both homozygous lines, and an increase was observed in hemizygous lines compared to the nontransgenic line. SNRK3.8 is a CBL-interacting protein kinase (CIPK), which acts in Ca^{2+} signaling and might have roles in abiotic and biotic stress response and ABA signaling (Kanwar et al., 2014; Xu et al., 2016). In our dataset, SNRK3.8 had reduced levels in the homozygous and T6 hemizygous lines compared to the nontransgenicline, which could be related to suppression of ABA response. SAL1 (inositol polyphosphate 1-phosphatase) has a double function with

inositol polyphosphate 1-phosphatase and 3′(2′),5′-bisphosphate nucleotidase enzymatic activities (Quintero et al., 1996). By regulating IP3 levels, it was proposed to act as a negative regulator of ABA and stress responsive genes (Xiong et al., 2001). Moreover SAL1 was identified to have role in regulation of auxin response via inositol signaling and to be required for leaf vascular development (Robles et al., 2010). In our study SAL1 level in the T6 homozygous line was reduced compared to the nontransgenic line. Reduction of SAL1 levels could be associated with regulation of ABA and auxin signalling by high CK levels.

Gibberellins (GAs) are known to inhibit the CK response but CKs were not reported to inhibit the GA response (Fleishon et al., 2011). GA2OX6 (gibberellin 2-oxidase 6) has a role in inactivation of C19 gibebrellins (Rieu et al., 2008). Two GA2OX6 paralogs had reduced levels in the T6 homozygous line. GASA1 is a GA responsive gene having a role in cell elongation (Ben-Nissan and Weiss, 1996). GASA1 was suppressed in the T6 homozygous line.

1-aminocyclopropane-1-carboxylate oxidase (ACO4) is a key enzyme with a role in ethylene synthesis, which has role in fruit maturation in tomato and also in senescence (Johnson and Ecker, 1998; Li et al., 2011). ACO4 levels were increased in the T6 homozygous line compared to the nontransgenic line, which could be associated with senescence.

PP2A (protein phosphotase 2A) is a signaling protein having a role in PIN protein targeting through vesicular transport for regulation of auxin distribution (Michniewicz et al., 2007). Moreover the PP2A regulatory subunit was identified to be targeted to peroxisomes and shown to regulate β-oxidation of fatty acids (Kataya et al., 2015). In our study the PP2A regulatory subunit was upregulated in the T6 homozygous line compared to the non-trangenic line. Upregulation of PP2A in the T6 homozygous line could be associated to auxin hormone distribution regulation or β-oxidation of fatty acids.

MES3 (Methylesterase 3) paralogs have methyl esterase activity on methyl indole-3-acetic acid (MeIAA), methyl jasmonate (MeJA) and methyl salicylate (MeSA) (Yang et al., 2008; Koo et al., 2013). MES3 has a high similarity to SABP2 which is a SA binding protein with MeSA methyl esterase activity and required for systemic acquired resistance (Forouhar et al., 2005; Koo et al., 2013). In our dataset, MES3 was strongly induced in both homozygous lines and the T6 hemizygous line compared to the nontransgenic line. VDAC1 (voltage dependent anion channel 1) is a mitochondrial

outer membrane protein having a role in metabolite transport between mitochondria and cytoplasm (Kroemer et al., 2007). Moreover VDAC1 has a role in pathogen defence by regulating H_2O_2 generation in *Arabidopsis* (Tateda et al., 2011). VDAC proteins were induced by SA in pearl millet (Desai et al., 2006). VDAC1 had significantly higher levels in the T6 homozygous line compared to the nontransgenic line. Increased levels of VDAC1 and MES3 could be associated with increased SA levels in the homozygous line.

The interaction mechanisms between CK and jasmonic acid (JA) signalling pathways are not clear. Some contradictory results were reported for regulation of the JA pathway by CKs. Exogenously applied CK and JA were identified to regulate leaf senescence antagonistically in *Oryza sativa* (Liu et al., 2016). Increased CK levels were identified to cause an increase in JA metabolites such as 12-oxo-phytodienoic acid (OPDA) (Schäfer et al, 2013). Moreover, increased JA levels were observed in tobacco plants with excessively high CK production (Novák et al., 2013). In *SAG::IPT Arabidopsis* plants under control conditions, JA levels were reduced compared to nontransgenic plants, whereas JA levels increased under drought stress conditions (Prerostova et al., 2018). Jasmonic acid biosynthesis initiates with hydrolytic cleavage of α-linolenic acid (18:3) and hexadecacatrienoic acid (16:3) fatty acids form membrane lipids. LOX catalyses the introduction of oxygen into 18:3/16:3 fatty acid chains and produces the substrate molecules which are then converted by allene oxide synthase to allene oxide. In our study, two LOX2 (lipxygenase) paralogs had significantly reduced levels in the T6 homozygous line compared to the nontransgenic line. Allene oxide can be spontaneously cyclised or enzymatically cyclised by allene oxide cyclase (AOS) to OPDA/np OPDA products (Schaller et al., 2009). In our study AOC3 (allene oxide cyclase) was upregulated in both T6 and T19 homozygous and hemizygous lines compared to the nontransgenic line. OPDAs/npOPDAs are intermediate metabolites of the JA biosynthetic pathway with signalling properties (Park et al., 2013; Taki et al., 2005). Synthesized OPDA/npOPDA are transported to peroxizomes for reduction and chain shortening via β-oxidation, then JA activation is ensured by amino acid conjugation (Wasternack and Song, 2016). Hydrogenperoxide lyase (HPL) is an enzyme acting parallel to AOS in the JA biosynthetic pathway. These enzymes compete with each other for the same substrates and HLP catalyzes aldehyde and oxoacid formation from fatty acid hydroperoxides (Nilsson et al., 2016). Products of HPL are aroma and signaling molecules with diverse functions in abiotic and biotic stress

responses (Savchenko et al., 2013). In our study HPL1, a competitor of AOS for substrates, had reduced expression levels in the T6 homozygous line compared to the nontransgenic line. In our study two AOS (allene oxide synthase) paralogs also had decreased levels in T6 hemizygous lines compared to the nontransgenic line. In our study, we observed regulation of several enzymes in the JA biosynthetic pathway by increased CK levels, but not every detected biosynthetic enzyme was similarly regulated. Although two LOX2 and AOS paralogs were down regulated in the T6 homozygous line compared to the nontransgenic line, a JA biosynthetic enzyme, AOC, was strongly upregulated in all transgenic lines. This could result in increased OPDA/npOPDA levels in homozygous lines. Moreover regulation of some JA biosynthetic enzymes seems to be related to CK levels, for instance some enzymes (AOS and LOX) were regulated in only one of the homozygous lines but AOC3 was upregulated in both homozygous and hemizgous lines.

Although CKs are known as plant growth regulators they also have a role in plants' defence against pathogens in concert with salicylic acid (SA) signalling pathways. CKs are known to induce SA signalling (Naseem et al., 2012). Exogenous treatment with CKs or endogenous CK production are related to the induction of SA biosynthesis and signalling related proteins in different plant species (Choi et al., 2010; Argueso et al., 2012). In our dataset, we did not detect any enzyme or receptor for SA biosynthesis or signalling but we detected many proteins possibly induced by SA. Glutaminyl cyclase (QC) catalyses catalyze the conversion of glutamate residues to pyroglutamic acid (pGlu) at the N-terminus of some peptides and proteins (Schilling et al., 2007). Proteins containing pGlu were identified to have roles in the defence response and include PR proteins in plants (Seifert et al., 2009). pGlu conversion in PR proteins could have a role as a signal of pathogen stress (Seifert et al., 2009). In our study, a QC ortholog was strongly upregulated in the T6 homozygous line compared to the nontransgenic line. Strong overexpression of QC could be a sign of heavy metabolic stress in the T6 homozygous line inflicted by high CK levels, which could be related to induction of SA signalling. IBI1 encodes an aspartyl tRNA synthase acting as a producer for beta-aminobutyric acid (BABA), which is a plant defence activator (Luna et al., 2014). BABA is a chemical, priming SA-induced defence response (Cohen, 2002). In our study, IBI1 levels increased in homozygous lines compared to the nontransgenic line. Increased levels of IBI1 could be associated with activation of the SA pathway in homozygous lines. Pathogenesis-related protein STH-2 is a PR-10

protein having a ribonuclease activity and activated under different stress conditions such as pathogen attack and abiotic stress conditions (Liu et al., 2006). STH-2 was upregulated in homozygous lines compared to the nontransgenic line. ALD1 is an aminotransferase synthesizing pipecolic acid form lysine. Pipecolic acid is related to systemically acquired resistance (SAR) and loss of function mutants were identified to be hypersusceptible to pathogenic bacteria (Song et al., 2004). SAR is known to be related to SA signalling. In our study levels of ADL1 were reduced in homozygous lines and the T6 hemizygous line, which could be related to induction of SA signalling in transgenic lines with high CK levels.

1.4.7. DNA and RNA Binding Proteins

AGO (argonaute) is an enzyme with a role in siRNA mediated gene silencing and has a small RNA-guided endonuclease activity for target mRNA (Voinnet, 2009). AGO2 has a role in RNA silencing mediated virus defence mechanisms (Jaubert et al., 2011). In our study AGO2 was downregulated in both homozygous lines compared to the nontransgenic line. AGO4 is an enzyme with roles in siRNA-mediated gene silencing, RNA-directed DNA methylation for heterochromatin formation and siRNA-mediated virus defence (Rowley et al., 2011; Oliver et al., 2016; Brosseau et al., 2016). In our study AGO4 had increased levels in both homozygous and T6 hemizygous lines compared to the nontransgenic line. AGO4 could be positively regulated by CKs and could have a role in regulation of CK mediated gene expression via chromatin remodeling. AGO1 is an enzyme with roles in siRNA-mediated gene silencing and in regulation of gene expression during senescence (Qin et al., 2016). AGO1 was upregulated in the T6 homozygous line compared to the nontransgenic line, which could be related to high CK induced stress and senescence. SMFA (small nucleolar ribonucleoprotein F A) is a component of the splicesome complex and could have a role in the splicing pattern of mRNAs in *Arabidopsis* (Kanno et al., 2017). In our study SMFA was upregulated in the T6 homozygous line compared to the nontransgenic line, which could cause changes in mRNA splicing and, as a result alter gene expression. DEAD-box protein UAP56 is a RNA helicase with a role in mRNA splicing and mRNA

transport (Kammel et al., 2013). In our study UAP56 was upregulated in homozygous transgenic lines compared to the nontransgenic line. Increased levels of UAP56 could be related to changes in mRNA splicing and transport caused by increased CK levels.

CSP41A and CSP41B (chloroplast stem-loop binding protein of 41 kDa) are proteins with ribonuclease activity having a role in plastid rRNA maturation (Bollenbach et al., 2009). In our study CSP41A and CSP41B were downregulated in homozygous lines and the T6 hemizygous line compared to the nontransgenic line. Reduction in CSP41A and CSP41B levels could be associated with reduced rRNA and assembled ribosomes and, as a result, reduced protein translation in high CK expressing lines, which could result from stress.

RNA binding proteins have diverse roles in cellular processes mainly in RNA metabolism via regulating RNA stability especially under different developmental and stress conditions (Lorković et al., 2009). GR-RBP2 (glycine-rich RNA-binding protein 2) is a protein acting as RNA chaperone and conferring abiotic stress tolerance in *Arabidopsis* (Kim et al., 2006; Yang et al., 2014). RGGA (hyoluranon mRNA binding family) is a mRNA binding protein locating in transpiration controlling organs such as stomata (Ambrosone et al., 2015). Knockout mutants of RGGA caused hypersensitity to ABA in *Arabidopsis* and its overexpression conferred tolerance to ABA, drought and salinity (Ambrosone et al., 2015). AtRZ-1 is a zinc finger-containing glycine-rich RNA binding protein having a role in cold and freezing via acting as a RNA chaperone, however, this protein does not confer tolerance to drought or dehydration stress (Kim et al., 2007; Kim et al., 2010). In our study GR- RBP2, RGGA and AtRZ-1 protein were upregulated in the homozygous line compared to the nontransgenic line. GR-RBP2, RGGA and AtRZ-1 protein levels could be increased in response to the increased stress imposed by high CK levels. GRP7 is a glycine-rich RNA binding protein which has a role in circadian clock regulation, plant immunity and cold stress (Meyer et al., 2017). Levels of GRP7 were reduced in homozygous lines compared to nontransgenic line. FIP (factor interacting with Poly(A) polymerase) is a component of the polyadenylation complex which determines mRNA fate (Helmling et al., 2001). Loss of function FIP1 mutants in *Arabidopsis* caused enrichment of ABA responsive genes and abiotic stress response genes (Telléz-Robledo et al., 2019). In our study, FIP1 levels were very strongly reduced in T6 homozygous compared to nontransgenic lines. Reduction of FIP1 levels could be associated with induction of ABA response and abiotic stress related genes in the highly CK expressing line.

BRCT domain-containing DNA repair protein has a role in non-homologous end joining (NHEJ) repair to double strand DNA damage (Leung and Glower, 2011). In *Arabidopsis* the BRCT domain-containing DNA repair protein was strongly induced by nutrient deficiency (Nishida et al., 2017). In our study BRCT domain-containing DNA repair protein levels increased in both homozygous lines compared to the nontransgenic line. BRCT domain-containing DNA repair protein could be positively regulated by CKs as it had increased levels in all transgenic lines.

Histone (HT) composition and modification is of great importance for chromation organization and gene expression as a result of cell type and developmental stage identity (Li and Workman, 2007). The nucleosome is the core structural building block of chromatin composed of four core histones: H2A, H2B, H3 and H4 (Luger et al., 1997). In our study HTB2, HTB4 and HTB1 had increased levels in homozygous lines compared to the nontransgenic line, whereas H4 was downregulated in the T6 homozygous line. Changed expression levels of histone proteins could be associated with altered chromatin structure and gene expression in high CK expressing transgenic lines.

1.4.8. Amino Acid Metabolism

Nitrogen is an essential macronutrient for plants and is an essential component of amino acids, nucleic acids, small molecules such as hormones and enzyme prosthetic groups (Marschner, 2011). N can be absorbed from soil in nitrate, urea and ammonium forms by plants and ammonia is assimilated by the glutamine synthase (GS)/gluatamate synthase (GLU1) pathway (Lea and Miflin, 2011). Absorbed ammonia is transferred into glutamate or glutamine and the ammonia released from the GS reaction is utilized for further amino acid biosynthesis or other nitrogen containing metabolites via amination reactions (Foyer et al., 2011). GDH (glutamate dehydrogenase 1) is another enzyme which could directly bind ammonia to 1-oxoglutarate for glutamate biosynthesis and ammonia assimilation (Foyer et al., 2011). GLU1 has roles nitrogen assimilation and re-assimilation of ammonia produced during photorespiration (Feraud et al., 2005; Jamai et al., 2009). GLU1 loss of function mutants exhibited stress related

gene expression including down-regulation of photosynthesis (Kissen et al., 2010). GDH1 could take part in ammonia assimilation or glutamate deaminatin depending on C (carbon) and N (nitrogen) availability (Miyashita and Good, 2008). Moreover GDH was identified to be strongly induced under stress condition (Chaffei et al., 2004). In our study GDH1 levels were upregulated in the T6 homozygous line, which could be an indicator of increased stress levels in the high CK producing homozygous line. GLU1 levels were reduced in the homozygous and T6 hemizygous lines. GS1 and GS2 (glutamine synthase) isoforms are known to have roles in the nitrogen remobilization processes (Moison et al., 2018). In our study GS1 and GS2 levels were downregulated in homozygous and T6 hemizygous lines compared to the nontransgenic line.

ACT domain repeat (ACR) proteins are allosteric regulatory protein domains controlling the activity of amino acid biosynthetic enzymes including aspartate kinase (AK), chorismate mutase (CM) and TyrA (prephenate dehydrogenase, PDH) (Liberles et al., 2005). ACR11 was identified to control activity of GS2 and GLU1 in *Arabidopsis* as loss of fuction mutants exhibited reduced activity of GS2 and GLU1 (Osanai et al., 2017; Takabayashi et al., 2016). In our study levels of two ACR11 isoforms were downregulated in homozygous lines compared to the nontransgenic line. We also observed reduced levels of GS2 and GLU1, which are ACR11-regulated enzymes.

Serine is a significant amino acid acting as a precursor for biosynthesis of other aminoacids such as cysteine and methionine, and cysteine is used as a precursor for synthesis of the antioxidant glutathione (Ros et al., 2014). PGDH (phosphoglycerate dehydrogenase) is a component of the phosphorylated pathway of serine (PPSB), which is the second serine biosynthetic mechanism after glycolate pathway (Ho and Saito, 2001). PPSB was identified to be the only source for serine in tissue distant to vasculature (Toujani et al., 2013). Serine accumulated under abiotic stress conditions in plants and has a role in stress tolerance (Rosa-Téllez et al., 2020). As serine is the only precursor for cysteine biosynthesis and sulfide fixation, PGDH is important for sulfide fixation (Anoman et al., 2019). OASA1 (O-acetylserine (thiol) lyase isoform A1) is an enzyme with a role in cysteine biosynthesis and inorganic sulfide fixation . OASA1 expression was identified to be induced by abiotic stress mediated by ABA (Domínguez-Solís et al., 2001). OASC is an isoform of O-acetylserine (thiol) lyase with a role in cysteine biosynthesis. OASC was also identified to be involved in cyanide detoxification in mitochondria, which is produced during ethylene and phytoalexin biosynthesis (Álvarez et al., 2012). In our study PGDH1 and PGDH2 were upregulated

in homozygous lines compared to the nontransgenic line. Moreover OASA1 and OASC were upregulated in the T6 homozygous line compared to the nontransgenic line. Induction of OASA1 and OASC could be related to increased stress in the high CK producing homozygous line. Upregulation of the abovementioned serine and cysteine biosynthetic enzymes could be related to the increased stress levels in homozygous lines compared to the nontransgenic line.

Aspartate aminotransferase (ASP) has a role in the formation of aspartate by transamination between glutamate and oxaloacetate. ASP has a significant role in channeling nitrogen to aspartate from glutamate (Wilkie and Warren, 1998). ASP5 was hypothesized to be involved in shuttling of reducing equivalents (Liepman and Olsen, 2003). In our study ASP2 and ASP5 had increased levels in the homozygous lines compared to the nontransgenic line.

P5CDH is an enzyme catalyzing the second step of proline catabolism to glutamate. Accumulation of the proline degradation intermediate P5C was identified to be related to ROS and HR response (Deuschle et al., 2004). Increased levels of P5CDH are associated with reduced ROS as it degrades P5C to glutamate (Miller et al., 2009). P5CDH levels increased in senescing plant leaves, which could be associated with proline catabolism induction (Faës et al., 2015). In our study the level of P5CDH was increased in homozygous lines compared to the nontransgenic line, which could be related to increased proline catabolism and senescence in high CK producing mature leaves.

Glycine cleavage T-protein and GLDP1 (glycine decarboxylase P-protein 1) are components of the mitochondrial glycine cleavage system which has a role in one carbon metabolism and photorespiration. Photorespiration is active in all photosynthesing tissues and one carbon metabolism is active in highly biosynthetic tissues (Engel et al., 2007). The glycine cleavage system acts in concert with serine hydroxymethyltransferase (SHM) to contribute to both one carbon metabolism and photorespiration (Douce et al., 2001). In our study, the levels of glycine cleavage T-protein, GLDP1 and SHM were reduced in homozygous lines compared to the nontransgenic line. Reduction of the abovementioned enzyme levels could be related to reduction in photorespiration, photosynthesis and biosynthetic reactions in homozygous lines with high CK levels. Other photorespiration and glyoxalate cycle related enzymes are alanine:glyoxylate aminotransferases (ALAATs), which link mitochondrial glycolate oxidation to the major photorespiratory pathway (Niessen et al., 2012).

Increased ALAAT levels were identified to be associated with improved conversion of glycolate to glycine and use of glycine (Niessen et al., 2012). In our study ALAAT levels increased in the T6 homozygous line compared to the nontransgenic line, which could be associated with increased glycine levels. Ala:2-oxoglutarate aminotransferase 2 (GGT2) is another photorespiratory aminotransferase located in peroxisomes catalyzing a transamination reaction in different substrate pairs such as (Glu):glyoxylate, Ala:glyoxylate, Glu:pyruvate, and Ala:2-oxoglutarate (Liepman and Olsen, 2003). AGT1 (alanine:glyoxylate aminotransferase) is another peroxisomal respiratory aminotransferase working on substrate pairs such as Ser:glyoxylate, Ala:glyoxylate, Asn:glycolate (Zhang et al., 2013). In our study two isozymes of AGT2 and AGT1 had reduced levels in homozygous and T6 hemizygous lines.

CARA (carbamoyl phosphate synthase) is an enzyme with a role in conversion of ornithine into citruline for arginine and pyrimidine biosynthesis (Kafer et al., 2004; Slocum, 2005). In our study, CARA levels increased in both homozygous lines compared to the nontransgenic line. Upregulation of CARA protein could be associated with regulation of arginine amino acid metabolism. Argininosuccinate synthase (ASS) is the rate limiting enzyme catalyzing conversion of citruline to arginine and is one of the key enzymes regulating arginine metabolism (Slocum, 2005). In our study, AS levels increased in the T6 homozygous line compared to the nontransgenic line, which could be related to increased arginine levels in the T6 homozygous line.

Glutamate decarboxylase (GAD) is an enzyme catalyzing decarboxylation of glutamate to γ aminobutyrate. GAD has a calmodulin binding domain which activates GAD under high calcium levels in response to different stress types (Gut et al., 2009). In our study GAD levels increased in the T6 homozygous line compared to the nontransgenic line which is an indicator of stress caused by high CK levels.

1.4.9. 14-3-3 Proteins

14-3-3 proteins, which are also named as general growth regulatory factors (GRFs) have diverse roles in regulation of cellular processes including metabolism, cell cycle, signal transduction and stress response (Mackintosh, 2004).*Arabidopsis* 14-3-3

proteins are divided into epsilon and non-epsilon groups. The epsilon group has five isoforms: mu, epsilon, pi, iota and omicron. The non-epsilon group has eight isoforms: kappa, lambda, psi, nu, upsilon, omega, phi and chi (Ferl et al., 2002). GRF9 was identified to be involved in P deficiency response in *Arabidopsis* and overexpression of *Arabidopsis* GRF9 in tomato conferred tolerance against P deficiency and improved yield and plant growth (Cao et al., 2007; Zhang et al., 2018). GRF2 was identified to regulate MAP kinase phosphatase in barley (Ghorbel et al., 2017). GRF1 was identified to be involved in C/N nutrient response interactions with ATL31 ubiquitin ligase (Sato et al., 2011). GRF11 was identified to have a role in iron acquisition interaction with nitric oxide (Yang et al., 2013). In our study, we detected several GRF proteins belonging to different subgroups of 14-3-3 proteins. Two paralogs of GRF1, GRF2, GRF7, GRF9 and GRF12 had reduced levels in the T6 homozgygous line compared to the nontransgenic line. As 14-3-3 proteins are involved in regulation of cellular processes such as metabolism, signalling and cell cycle, down regulation of various 14-3-3 protein paralogs in homozygous lines could be associated with increased metabolic stress in these lines.

1.5. Conclusion

We developed transgenic tomato plants over-expressing the *IPT* gene under control of the senescence and maturity inducible promoter SARK. We selected two independent transgenic lines in our study and used hemizygous (single trangene copy) and homozygous (double transgene copy) transgenic lines. We evaluated the phenotypic, growth and yield related parameters in our transgenic lines and nontransgenic line. Although all transgenic lines had similar patterns of vegetative growth and development resembling the nontransgenic line, after flowering various symptoms were observed. We observed a reduction in growth and yield related parameters in homozygous transgenic lines with a stunted growth habit and death in newly growing apex tissue. We also detected growth of adventitious shoots from the vascular tissue of homozygous lines. In hemizygous lines we also observed reduced yield (reduced flower and fruit number and fruit weight), whereas we observed an

increased biomass accumulation in green tissue. Moreover we observed improved water content in both homozygous and hemizygous lines. We observed more severe symptoms in the T6 homozygous line compared to the T19 homozygous line. The symptoms after flowering had a range of severity with the worst growth defects in the T6 homozygous line followed by the T19 homozygous line, the T6 hemizygous line and the T19 hemizygous line. The observed symptoms in our transgenic lines suggested that SARK was a leaky promoter that did not confer a strictly regulated expression pattern of the transgene. Also the array of symptom severity in the transgenic lines indicated that the lines had a gradient of *IPT* gene expression such that the T6 homozygous line had the highest levels, followed by the T19 homozygous line, the T6 hemizygous line with the lowest expression in the T19 hemizygous line. We conducted shotgun proteomic analysis from the mature leaf tissue collected from the different transgenic lines and nontrangenic plants. We identified 902 proteins with changed expression levels in at least one of the comparison group. We conducted PCA analysis for the collected leaf total proteome dataset. We identified that the T6 homozygous line was distinct from the rest of the tested lines in PCA analysis. The localization proximity of the tested lines can be inferred as the similarity in their leaf total proteomics data. PC1 discriminated the T6 homozygous from the rest of the tested lines in terms of proteomic expression pattern. Therefore the PC1 loadings with the highest and lowest values can most significantly describe the T6 homozygous line compared to the other lines. The 30 proteins with lowest loading scores in PC1 were those which were strongly downregulated in the T6 homozygous line. Most of the proteins in this group were photosynthesis related, chloroplast structural and protein metabolism related proteins and they were down-regulted in homozygous transgenic lines. The 30 proteins with highest loading scores in PC1 were those which were strongly upregulated in the T6 homozygous line. Most of the proteins with highest rotation values were stress responsive proteins and they were upregulated in homozygous transgenic lines. We also conducted clustering analysis from the proteomics data to separate the proteomics data according to the expression pattern between different test groups. Most of the anabolic proteins involved in photosynthesis, TCA, oxidative phoshorylation, amino acid biosynthesis, protein synthesis were grouped in clusters with reduced expression levels that were generally gradual in the T6 homozygous line, followed by the T19 homozygous T6 hemizygous lines compared to the nontransgenic line. Very few anabolic enzymes had reduced levels in the T19 hemizygous line compared to the

nontransgenic line. The gradually reduced levels of anabolic enzymes can be considered as an indicator of stress level in the lines which was associated with increased CK levels. Stress responsive proteins, such as those related to biotic and abiotic response, ER stress related proteins, detoxification related proteins, were strongly induced in the T6 homozygous line followed by the T19 homozygous line with fewer also upregulated in the T6 hemizygous line compared to the nontransgenic line. Again, this relationship suggests that these proteins were regulated in a CK level dependent manner. We also observed some interesting proteins which could have roles in CK signalling in the transgenic lines. In our transgenic lines we observed more prominent vascular tissue with increased stem diameter and larger veins in leaves. We detected proteins which could have roles in CK-dependent vascular tissue development such as sieve element-occluding protein paralogs, expansions, callose and cell wall biosynthetic enzymes like 1,3 glucan synthases. We also detected changes in the central carbon metabolism of homozygous lines with high CK levels, which implies a changed source/sink relationship. We detected increased levels of cell wall invertase, vacuolar invertase and reduced SUC2 (sucrose-proton symporter 2) which indicates that mature leaves of the homozygous lines with high CK levels were more inclined to hold onto the sugar produced as a result of photosynthetic activity rather than loading it into phloem for transport into young sink tissue. Mature leaves may even have unloaded sugar from phloem fluid. This strong sink phenotype of mature leaves could explain the apex death in homozygous lines, which could be associated with inadequate photosynthetic assimilate reaching the young tissue which had low photosynthetic efficiency and high demand for growth and development. This inadequate photosynthetic assimilate transport to young tissue could result in starvation and eventually death of that tissue in the apex. In our study we also observed increases in pathogenesis related (PR) protein levels in the homozygous line with high CK levels. PR proteins were previously identified to be related to the HR (hypersensitive response) induced by SA signaling. In future studies, the CK levels in the transgenic lines should be measured to verify if the homozygous lines have significantly higher levels of CKs, in correlation with the invoked phenotypic changes. It can then be tested if the death in the apex induced by high CK levels resulted from starvation induced by the strong sink properties of mature leaves or caused by a HR response induced by PR proteins. To test the contribution of starvation in young sink tissue death at apex caused by changes source/sink relationship in transgenic, the levels of SNRK1, low energy marker levels could be measured by

RT-qPCR moreover the sucrose levels in phloem sap can be measured via mass spectrometry based methods and compared with nontransgenic. To test the contribution of HR like response in young leaf death caused HR markers such as PR protein transcript levels could be measured by RT-qPCR moreover the oxidative stress levels can be monitored by hydrogen peroxide and superoxide levels by staining methods.

CHAPTER 2

PROTEOMIC PROFILING OF DROUGHT STRESSED TOMATO PLANTS OVEREXPRESSING CYTOKININS

2.1. Introduction

2.1.1. Drought Stress

Drought is the most damaging abiotic stress affecting crop production and causing losses more than all other causes combined (Foolad, 2007). Moreover, it is reported that 45% of the land surface is subject to water stress (Tanji, 1990). Thus, drought is the most severe problem for agriculture. Drought stress causes reduced photosynthesis and cell division and increased leaf senescence, thus causing reduced crop plant quality and yield (Munns, 2002). Drought stress tolerance is a complex phenomenon, controlled by multiple genes and influenced by uncontrollable environmental factors (Vinocur and Altman, 2005). Furthermore, stress tolerance mechanisms depend on plant developmental stage (Foolad, 2007). Because of this complexity, drought stress tolerance is a difficult character to improve via conventional breeding methods in crop plants. Drought stress causes dehydration in plantswhich causes osmotic stress; then osmotic stress invokes further damage in cells andplant tissues. As a result, yield and quality losses are seen (Wang et al., 2003). Osmotic stress also disrupts homeostasis and ion distribution in the cell (Zhu, 2001). Osmotic stress is a shared component of drought, salt and freezing stresses causing induction of similar molecular response pathways. Moreover, dehydration stress causes oxidative stress which induces damage in cell membrane lipids and also disrupts the cell's functional and structural proteins (Smirnoff, 1998). The initial plant response to dehydration stress is activation of signalling pathways to adapt metabolism for survival in a changing

environment (Zhu, 2002). Plants exposed to water restriction deal with the problem via adjusting root growth, regulating transpiration via stomatal adjustment and cell membrane changes for improving water availability and usage efficiency (Feng et al., 2016; Zhu, 2016). Moreover, plants tolerate the harmful effects of drought by activating several biochemical responses such as the synthesis and accumulation of osmoprotectants, accumulation of protective proteins (heat shock proteins, LEA, etc.), maintenance of intracellular ion homeostasis, and expression of proteins and small molecules for scavenging of reactive oxygen species (ROS) (Ashraf and Akram, 2009). The abovementioned changes in the biochemical responses of the plant mainly depend on hormonal changes, especially in abscisic acid (ABA) and cytokinins (CKs) (Davies and Zhang, 1991), which activate several transcription factors (CBF/DREB and NF-Y) and vice versa (Nelson et al., 2007; Zhang et al., 2004). ABA is the primary hormone controlling the response to drought stress. However, the plant abiotic stress response can be mediated by both ABA-dependent and independent pathways. In the ABA-dependent pathwayunder stress conditions, ABA binds to its receptor REGULATORY COMPONENTS OF ABA RECEPTOR (RCAR) [original name PYRABACTIN RESISTANCE 1 (PYR1)/PYR1-LIKE (PYL)], which are START family receptors. Binding of ABA to RCAR inhibits the phosphatase activity of the receptors enabling the autophosphorylation of SnRK2 (NON-FERMENTING-1 (SNF1)-RELATED PROTEIN KINASE) (Fernando et al., 2013). SnRK2 is activated by phosphorylation and causes phosphorylation of the ABA responsive transcription factor ABSCISIC ACID-RESPONSIVE ELEMENT (ABRE) BINDING PROTEINs [(AREBs)/ABRE BINDING FACTORs], which regulate the downstream ABA response (Joshi et al., 2016). Hormonal changes in response to drought cause inhibition of photosynthesis (Chaves, 1991). Decreased photosynthesis is caused by reduced CO_2 diffusion due to decreased stomatal conductance to minimize water loss (Munns, 2008). This reduction in photosynthesis is an important cause of decreased yield in response to drought. Moreover, the hormonal balance change in response to drought causes an initial reduction in shoot growth followed by accelerated senescence, which is directly related to decreased levels of CKs (Ghanem et al., 2008). Moreover, severe stress conditions like drought cause induction of premature senescence which results in reduced photosynthesis and yield in crop plants (Gregersen et al., 2013).

2.1.2. Role of CKs in Drought Stress Response

As mentioned above, drought causes decreased CK levels, due to differential regulation of *IPT* and *CKX* gene expression (Nishiyama et al., 2011, Le et al., 2012, Ramireddy et al., 2014). Drought not only reduces the expression levels of the CK biosynthetic gene *IPT* but also the CK signalling genes which act positively on the CK response (Nishiyama et al., 2013). There are contradicting results about the effect of CK on drought tolerance. Some studies indicated that CK acts as a negative regulator of drought stress (Nguyen et al., 2016; Nishiyama et al., 2013), whereas some studies indicated that increased CK levels could contribute to drought stress tolerance (Rivero et al., 2007; Marewitz et al., 2011; Reguera et al., 2013). Decreased CK content and signalling are associated with increased sensitivity to the stress hormone ABA and reduction in shoot growth which are related to adaptation and survival under drought stress, but limit the yield for crop plant production (Tran et al., 2007; Werner et al., 2003).

Studies that showed a negative effect of CKs on drought tolerance, generally demonstrated a positive contribution of impairment of CK biosynthetic enzymes or CK signalling repressor genes (Li et al., 2016). Mutation in CK receptors (AHK2, AHK3) or positive signalling components such as HPT (AHP2, AHP3, AHP5) and RRB (ARR1, ARR10, ARR12) exhibited improved drought tolerance (Nyungen et al., 2016; Nishiyama et al., 2011). Drought tolerance caused by CK reduction was observed to be related with improved cell membrane integrity, decreased stomatal aperture and increased ABA sensitivity (Nyungen et al., 2016). The CK signalling negative regulator *RRA* genes (*ARR5, 6, 7, 15, 22*) were upregulated under cold and salt stresses, indicating a similar response mechanism (Jeon and Kim, 2013;Kim et al., 2013). Overexpression of type-A *ARR22* improved drought tolerance (Kang et al., 2013). ABA signalling induces MYB2 and decreases *IPT* expression thus reducing CK concentrations (Guo and Gan, 2011). As expected, reduction of CK levels decreases the output of the CK signalling pathway and signalling components (AHK, AHP, ARR). Type B ARRs (ARR1, 11 and 12) interact with SnRNK2 and repress them under nonstress conditions, whereas reduced CK levels cause decreased levels of the aforementioned ARRs, causing activation under drought stress (Huang et al., 2018). Moreover, when SnRNK2

is activated in response to CK reduction, it phosphorylates the type A ARR5, then further reduces CK signalling and represses growth (Huang et al., 2018).

Drought tolerance improvement by direct reduction of CK levels by overexpression of the *CKX* gene was also reported in different plant species. This type of drought tolerance could be related to reduction of the negative regulatory effect of CKs over root growth and branching (Werner et al., 2003). Overexpression of the *CKX* gene in a root tissue-specific manner reduced CK levels in the roots, thus improving the root growth and biomass without a significant change in shoot tissue (Macková et al., 2013, Werner et al., 2010). Transgenic plants overexpressing the *CKX* gene in root tissue adapted better to drought stress conditions and had improved survival rates compared to nontransgenic lines (Werner et al., 2010). Barley plants overexpressing *CKX* in a root tissue-specific manner suffered less from drought stress and had higher CO_2 assimilation rates related to increased stomatal conductance and lower ABA levels as a resultof decreased induction of the ABA-dependent signalling pathway (Ramireddy et al., 2018). Improved tolerance shown in the abovementioned studies could be caused by an improved root system, thus allowing plant roots to reach a higher volume of soil for water and mineral uptake, which could cause a reduction in metabolic stress and altered crosstalk between CK and ABA (Ramireddy et al., 2018).

Other studies have shown a positive effect of increased CK levels over drought stress tolerance. Controlled expression of the *IPT* gene, especially under maturation, senescence and abiotic stress inducible promoters has been reported to promote drought and other abiotic stress tolerance (Kant et al., 2015; Kuppu et al., 2013; Macková et al., 2013; Merewitz et al., 2012; Peleg et al., 2011; Qin et al., 2011). One of the most successful promoters for controlled expression of the *IPT* gene is SARK (senescence associated receptor kinase), which is induced by maturation and senescence (Delatorre et al., 2012). Effect of pro*SARK::IPT* overexpression on drought stress was first demonstrated in tobacco plants (Rivero et al., 2007). They observed improved survival and recovery rates under drought stress conditions with a water supply restriction as low as 30% of the normal watering conditions. The authors concluded that the positive effect of increased CK levels delayed the leaf senescence inflicted by drought stress. In another study, pro*SARK::IPT* overexpression induced a CK increase that protected the photosynthetic apparatus from damage and prevented degradation of its components under drought stress (Rivero et al., 2010). Overexpression of pro*SARK::IPT* in many different plant species such as cassava, rice, peanut, creeping bentgrass, cotton and

maize caused improved drought stress tolerance as observed in previous studies related to delayed leaf senescence (Zhang et al., 2010; Peleg et al., 2011; Reguera et al., 2013; Qin et al., 2011; Merewitz et al., 2012; Merewitz et al., 2016; Kuppu et al., 2013; Oneto et al., 2016). Controlled *IPT* over-expression using different promoters was also observed to improve growth and tolerance traits under drought stress conditions in canola and bentgrass similar to the abovementioned studies (Kant et al., 2015; Xu et al., 2016). In addition, controlled *IPT* over-expression in bentgrass provided high heat stress tolerance (Xu et al., 2009).

2.1.2.1. Mechanisms of Drought Tolerance by CK Overexpression

As summarised in the previoussection, modulation of CK biosynthesis, degradation and signalling provides tolerance to drought stress. Different mechanisms were proposed to contribute to CK-mediated water deficit stress. These mechanisms are: improvement of the antioxidant system, protection of photosynthetic apparatus, plant growth and development modulation, regulation of water balance and cross-talk between CK and stress hormones for their regulation.

2.1.2.1.1. Enhanced Antioxidant System

Abiotic stress tolerance conferred by controlled CK increase is reported to be related o the induction of antioxidant system-related enzymes (Rivero et al., 2007; Rivero et al., 2009; Rivero et. al., 2010; Xu et al., 2010; Peleg et al., 2011). Moreover, in transcriptomic studies examining plants exposed to higher CK levels by endogenous or exogenous treatment, genes related to antioxidant response are overrepresented (Zwack and Rashotte, 2015). Conversely, the same effect is observed in CK deficient *IPT* gene (*ipt1, 3, 5, 7*) mutant plants which exhibit over-representation of antioxidant response-related genes (Nishiyama et al., 2012). Improved antioxidant potential in response to CK level modulation is hypothesized to be related to the protective effect of

antioxidants on chloroplast integrity and chloroplastic activities (Rivero et al., 2007; Zavaleta-Mancera et al., 2007; Ma et al., 2018).

2.1.2.1.2. Modulation of Photosynthesis

Maturation or stress-induced increases in CK levels are known to improve salinity and drought tolerance. This tolerance improvement is reported to be related to preserved photosynthetic activity under stress conditions compared to nontransgenic plants (Ghanem et al., 2011; Rivero et al., 2007; Rivero et al., 2009; Rivero et al., 2010; Reguera et al, 2013; Ma et al., 2018; Oneto et al., 2016). Preservation of photosynthetic activity is associated with improved or preserved chlorophyll levels, photochemical efficiency, electron transport rate, photochemical quenching, CO_2 assimilation rates and increase in expression of genes related to photosynthetic processes. The opposite effect is reported in plants overexpressing the *CKX* gene, which is a CK degradation enzyme. These plants have decreased CK levels and a reduction in CO_2 assimilation rates caused by reduced stomatal conductance (Vojta et al., 2016). However, *CKX* overexpression guided with a different promoter resulted in increased CO_2 assimilation rates and increased tZ-type CK levels, which could be related to increased CK biosynthesis in different organs of the plants, thus contributing to photosynthetic activity (Ramireddy et al., 2018).

2.1.2.1.3. Modulation of Plant Growth and Development

CKs are one of the major hormones controlling root and shoot development and growth. Increased CK levels are known to decrease the root to shoot ratio (Laplaze et al., 2007; Novak et al., 2015). It is known that higher root biomass and improved root architecture can enable the plant to mine a higher volume of soil for water and mineral uptake (Passioura, 1985). Root specific overexpression of the *CKX* gene improvedroot architecture, growth, nutrient uptake and conferred tolerance to drought and salt stress

(Ramireddy et al., 2018; Pospíšilová et al., 2016; Werner et al., 2010; Ghanem et al., 2010). Dehydration responsive element binding factor (DREB) in Malus plants induced *CKX* expression in roots and drought tolerance (Liao et al., 2017). Moreover, xylem development was shown to be regulated by drought via the antagonistic relationship of CK and jasmonic acid (Jang et al., 2018). Root induced *CKX* epression was hypothesized to confer drought tolerance not only with enhanced lateral root growth and biomass but also with increased lignification observed in root tissue (Pospíšilová et al., 2016).

2.1.2.1.4. Regulation of Water Balance

Improved water uptake and reduced water loss by transpiration are significant mechanisms for drought tolerance. As mentioned in the previous section, reduced CK levels in root tissue cause increased root growth and lateral root formation resulting ingreater root biomass and improved root architecture. Moreover, reduced CK levels in root tissue are also associated with reduction in transpiration as a result of reduced stomatal conductance (Nguyen et al., 2016; Vojta et al., 2016; Liao et al., 2017). Interestingly, improved drought tolerance is achieved when the *IPT* gene is overexpressed in a maturation or stress-induced way, even though this change is accompanied by increased transpiration and stomatal conductance (Le et al., 2012; Reguera et al., 2013).

2.1.2.1.5. Crosstalk with Stress Hormones

ABA is the major hormone controlling the abiotic acid stress response including growth modification, synthesis of protective metabolites and stomatal closure; and its levels and signalling components are induced under drought stress. ABA and CKs are known to act antagonistically, for instance, ABA inhibits CK signalling and CK induces the degradation of the ABA signalling component transcription factor ABI5 (Nguyen

and Emery, 2017; Guan et al., 2014). Under drought stress conditions, the levels of CKs are decreased or CK signalling is attenuated, and these plants have lower levels of ABA but higher sensitivity to ABA (Nguyen et al., 2016; Nishiyama et al., 2011; Prerostova et al., 2018). SnRNK2, which is a key component of ABA signalling, is also negatively controlled by ARRs (ARR1, 11, 12) (Huang et al., 2018). The interaction of ABA and CK hormones modulated by SnRNK2 and ARRs balances stress defense and growth under abiotic stress conditions.

Another stress hormone having a role in drought tolerance is jasmonic acid (Ahmad et al., 2016). Jasmonic acid attenuates CK signalling by repressing the CK receptor AHK4 and inducing the negative CK regulator AHP6 (Jang and Choi, 2018). This negative regulation of CKs by jasmonic acid is associated with xylem differentiation and drought tolerance. Both low and high CK levels caused by *CKX* expression and *IPT* expression were demonstrated to increase jasmonic acid biosynthesis (Vojta et al., 2016; Novák et al., 2013).

2.1.2.1.6. Research Objectives and Work Flow

Increased CK levels caused by controlled *IPT* overexpression were previously found to confer tolerance for abiotic stresses such as drought, salinity and high temperature. The aim our work was to investigate the role of increased CK levels caused by IPT overexpression under drought stress conditions. For that aim we tested both nontransgenic and transgenic plants grown under control and drought stress conditions and evaluated some features such as plant height, plant fresh weight, MDA content, water use efficiency and detached leaf senescence. Leaf tissue is the primary target of CK action, thus we conducted the proteomic analysis in leaf tissue. Induction of the CK signalling pathway causes changes in gene expression in the nucleus by affecting transcription factors. Therefore, we aimed to investigate the role of increased CK levels on the nuclear proteome. For this goal, we conducted shot gun proteomic analysis in controland drought-stressed nontransgenic and transgenic plant leaf tissue at two levels: total soluble extracts and nuclei enriched extracts. We identified and quantified the proteins from nontransgenic and transgenic leaf total extract and nuclei

enriched extracts. The differentially abundant proteins between nontrangenic and transgenic lines grown under control and drought stress conditions were identified. We conducted functional annotation and characterization of the differentially abundant proteins. We also conducted clustering analysis for determination of expression pattern differences between groups (nontransgenic and transgenic grown under control or drought stress conditions). We identified proteins that could be controlled by CKs under drought stress. To our knowledge this is first report in tomato for investigation of the role of increased CK levels under drought stress and the molecular response to this stress at the leaf total and nuclei enriched proteome levels.

2.2. Materials and Methods

2.2.1. Whole Plant and Detached Leaf Drought Assays

Self-seeds from the T19 *SARK::IPT* transgenic line and nontransgenic Moneymaker were used for the analysis. Nontransgenic plants and *SARK::IPT* seeds were sown in soil which was pre-wetted and weighed and pots were covered with stretch film to prevent water loss. After germination of the seeds, holes were placed in the stretch film to allow plantlet growth. Each plant was watered to a level to keep the total pot weight constant in all tested plants. Plants were grown for 6 weeks in a growth chamber at 25^{o}C, 40% humidity and 16 h light 8 h dark cycle. After 6 weeks, control group plants were watered normally and drought stress group plants were left unwatered for 2 weeks. Plants were photographed and mature leaves (3rd fully expanded leaf from the apical meristem) were harvested for proteomics analysis and stored at -80^{o}C.

Detached mature leaves of untreated nontransgenic control and a *SARK::IPT* line (T19) were tested for leaf senescence. For this aim, detached leaves of the lines were placed in petri dishes containing damp filter paper and incubated at 20^{o}C in the dark for 7 days. Photographs of the incubated leaves were taken after 14 days. Leaf samples were collected at the beginning and end of the leaf senescence assay. Chlorophyll a and b levels were measured in the samples according to the method described by Warren (2008). Thus, 50 mg of leaf tissue was homogenized in 100%

methanol and the absorbance of the clarified solution was measured at 665 and 652 nm. Chlorophyll a and b contents were calculated using absorbance values and molar extinction coefficients.

2.2.2. Shoot Fresh Weight, Relative Water Use Efficiency and MDA Measurements

During the drought stress test, the pots were covered with stretch film to minimize water loss and the amount of irrigation water was recorded for each plant. After the drought stress tests, nontransgenic and T19 *SARK::IPT* plants grown under control and drought stress conditions were harvested and the fresh weights of their above ground tissues were recorded. Relative water use efficiency was calculated using the leaf fresh weight measurements and the amount of water used by each plant as total biomass/total water usage (Sharma et al., 2015).

Malondialdehyde (MDA) measurements were conducted from the mature leaves(3^{rd} fully expanded leaf from the apical meristem) of nontransgenic control and T19 *SARK::IPT* plants grown under control and drought stress conditions. MDA analysis was conducted based on the method explained by Heath and Packer (1968) from 100 mg leaf tissue. Absorbances of MDA-TBA complexes were measured at 532 and 600 nm and MDA contents were calculated using the molar extinction coefficient. Two way ANOVA and Tukey's HSD (honest significant difference) tests were carried out to evaluate the statistical significance of the differences between the groups using R software.

2.2.3. Analysis of Selected Metabolites

Amino acids and glutathione were isolated and analysed by LC-MS in a triple quad instrument (TSQ Quantiva, Thermo Fisher Scientific, USA) and a 15 cm Luna SCX column (2 mm inner diameter; Phenomenax, USA) according to the method

explained by Thiele et al. (2012). Analysis was conductedon two biological and three technical replicates of mature leaves (3rd fully expanded leaf from the apical meristem) of the nontransgenic control and T19 *SARK::IPT* plants grown under control and drought stress conditions. MS profiled data obtained from the LC-MS analysis was loaded in Skyline 3.1 (Skyline 3.1, MacCossLab Software, USA) and quantitative analysis was conducted based on area under the curve values.

Organic acid extractions and analysis were conducted based on the method of Roessner et al. (2000). Analysis was conductedon three biological and two technical replicates of mature leaves (3rd fully expanded leaf from the apical meristem) of the nontransgenic control and T19 *SARK::IPT* plants grown under control and drought stress conditions. For these meaurements, 100 mg plant tissue was homogenized and extracted in chloroform:methanol:water (1:3:1) mix containing 0.01% buthylated hydroxytoluene and dried samples were derivatized to obtain the trimethylsilylation product. The derivatized samples were analysed in a GC-2010 PluS Gas Chromatography instrument (Shimadzu, Japan) with a FID-2010 Plus Flame Ionization Detector (Shimadzu, Japan) and a Rtx-5 30m, 0.025mm ID and 0.25 μm df column (Restek, USA). Standard graphs were prepared from derivatized malic, lactic, pyruvic and citric acid standards. Concentrations of the samples were calculated using these standard graphs.

Fatty acid extractions and analysis were carried out according to the method described by Lissitsyna et al. (2012). Analysis was conductedon three biological and three technical replicates of mature leaves (3rd fully expanded leaf from the apical meristem) of the nontransgenic control and T19 *SARK::IPT* plants grown under control and drought stress conditions. For each sample, 100 mg leaf tissue was homogenized and extracted in dichloromethane: hexane (1:1) mix containing 0.01% buthylated hydroxytoluene. Isolated and dried fatty acid samples were converted to the corresponding fatty acid methyl esters by addition of methanol containing 10% (v/v) H_2SO_4. Samples were analysed with FAME standards in the gas chromatography instrument ionization detector described above and a Stabilwax-DA 60m, 0.25mm ID and 0.25 μm df column (Restek, USA). Fatty acid relative percentages were calculated based on peak areas.

Relative abundance values of the analysed metabolites were plotted in box plots using ggPlot2 package, R software (Wickham, 2016). Two way ANOVA and Tukey's

HSD (honest significant difference) tests were carried out to evaluate the statistical significance of the differences between the groups using R software.

2.2.4. LC-MS Proteome Profiling

Total leaf protein extraction was carried out in nontransgenic control Moneymaker (MM) and T19 *SARK::IPT* transgenic lines using a phenol protein extraction method (Carpentier et al., 2005). The extracted proteins were dissolved in lysis buffer (100mM Tris, 8M urea, 1% DTT) and protein concentrations were determined using Bio-Rad Protein Assay (Bio-Red, Hercules, CA, USA) as described by the manufacturer.

Leaf nuclear protein enrichment was conducted based on a modified procedure of percoll gradient centrifugation (Sikorskaite et al., 2013). Briefly, frozen (stored at -80^{o}C) leaf tissue was homogenized and clarified via filtration. Existing organelles were lysed with addition of 10% triton X-100 solution. Nuclei were collected by centrifugation through a 60% percoll cushion. Collected nuclei were re-washed with solution containing triton X-100 for removal of contaminant organelles. Isolated nuclei were visualised under the microscope with nuclei-specific DAPI staining. Protein isolation was carried out using TriPure Isolation Reagent (Roche, Germany) as described by the manufacturer. Resulting proteins were quantified using Bio-Rad Protein Assay (Bio-Red, Hercules, CA, USA) as described by the manufacturer.

Quantitative proteomic analyses of leaf total protein and leaf nuclear protein enriched extracts were performed using a gel-free shotgun protocol based on nano-HPLC and MS/MS in two biological replicates which were pooled from four plants and three technical replicates (Černý et al., 2013; Baldrianová et al., 2015). The extracted leaf total protein and leaf nuclear protein samples were digested in solution with immobilized trypsin beads (Promega, USA). The resulting peptides were desalted, dried and dissolved in 0.5% (v/v) formic acid in 5% (v/v) acetonitrile, then analysed by nanoflow C18 reverse-phase liquid chromatography using a 40 cm column (0.075 mm inner diameter; NanoSeparations) and a Dionex Ultimate 3000 RSLC nano UPLC system (Thermo Scientific, USA) directly coupled to a Captive Spray nanoESI source

(Bruker, Germany) and an UHR maXis impact q-TOF mass spectrometer (Bruker, Germany). Peptides were eluted with a 120min (maximum), 4% to 40% acetonitrile gradient. Spectra were acquired at 2 Hz per MS spectrum and in an intensity dependent mode for MS/MS spectra at a rate of 10-20 Hz with a total cycle time range of 7 seconds. Data from MS/MS data-dependent measurements were processed by Data Analysis 4.1 (Bruker, Germany) and searched against the Sol Genomics Network (SGN) *Solanum lycopersicum* combined unigene database downloaded in June 2016 (www.solgenomics.net), using Mascot 2.4 and Sequest HT (database search criteria: trypsin; variable modifications - methionine oxidation, NQ deamidation, acetylation and E/Q to pyro-Glu at N-terminus; ST phosphorylation; peptide tolerance - 35 ppm; allowed one missed cleavage; MS/MS tolerance - 0.1 Da) and Thermo's Proteome Discoverer 2.0 (target FDR<1%) to identify source proteins (using high-confidence peptides, $p < 0.05$ with at least one distinct proteotypic peptide per protein). Quantitative differences were assessed by a spectral counting method (e.g. Černý et al., 2013). Resulting candidates were then targeted via MRM-based analyses (Skyline 3.1, MacCossLab Software, USA) employing a similar LC interface connected to TSQ Quantiva (Thermo Fisher Scientific, USA) (four best scoring transitions; Q1 and Q3 resolution 0.7 Da; cycle time <4 seconds). Peptides were quantified based on the peptide ion signal peak areas obtained by targeted MRM analysis using Skyline software (Skyline 3.1, MacCossLab Software, USA). Quantitative differences were deemed significant if the drought stress/control ratio was ≥1.4 with *t*-test *P*-values <0.05.

Information about the functions of the identified proteins was collected from available literature and UniProt (http://www.uniprot.org/), MAPMAN (mapman.gabipd.org/) and PANTHER (http://www.pantherdb.org/databases) databases. The identified proteins were functionally annotated using the PANTHER database (http://www.pantherdb.org/).

2.3. Results

2.3.1. Development of Transgenic Tomato Lines and Confirmation of *IPT* Gene Expression

Transgenic plants were developed and *IPT* gene expression was confirmed as explained in chapter one.

2.3.2. Whole Plant Leaf Drought and Detached Leaf Senescence Assays

One of the transgenic T_0 line was used in experiments. T_1 plants were generated from the T_0 plants by self pollinating these lines. Transgenic T_1 lines were selected by PCR confirmation using *SARK::IPT* gene specific primers (data not shown). RT-qPCR experiments were conducted for these T_1 lines for selection of homozygous and hemizygous plants as explained in chapter one.

Drought stress tests were conducted on the *SARK::IPT* and nontransgenic MM plants. Under drought stress, nontransgenic plants experienced more severe dehydration compared to *SARK::IPT* plants as indicated by wilting (Figure 2.1). Nontransgenic plants became chlorotic and lost leaves, but *SARK::IPT* plants did not lose leaves or exhibit chlorosis, which are signs of senescence and stress. Also *SARK::IPT* plants were shorter than the nontransgenic plants. Overall, under drought stress conditions *SARK::IPT* plants retained better water status compared to nontransgenic plants. Detached leaves of the transgenic line retained their green color without any rotting; however, leaves from the nontransgenic lines became chlorotic and started to rot (Figure 2.3). Transgenic leaves retained healthy green status whereasthe leaves from the nontransgenic line experiencd faster senescence and tissue death. We also measured the chlorophyll content before and after the detached leaf senescence assay (2 weeks incubation) from the*SARK::IPT* and nontransgenic plants (Figure 2.3). In the nontransgenic line, fast chlorophyll a and b degradation was observed compared to

SARK::IPT leaves. Thus, a dramatic decrease in chlorophyll a and b levels occurred during the incubation period.

Figure 2.1. Nontransgenic and *SARK::IPT* plants grown under control and drought stress conditions. A: Plants grown under control conditions. B: Plants grown under drought stress conditions. On left: nontransgenic plants; on right *SARK::IPT* plants.

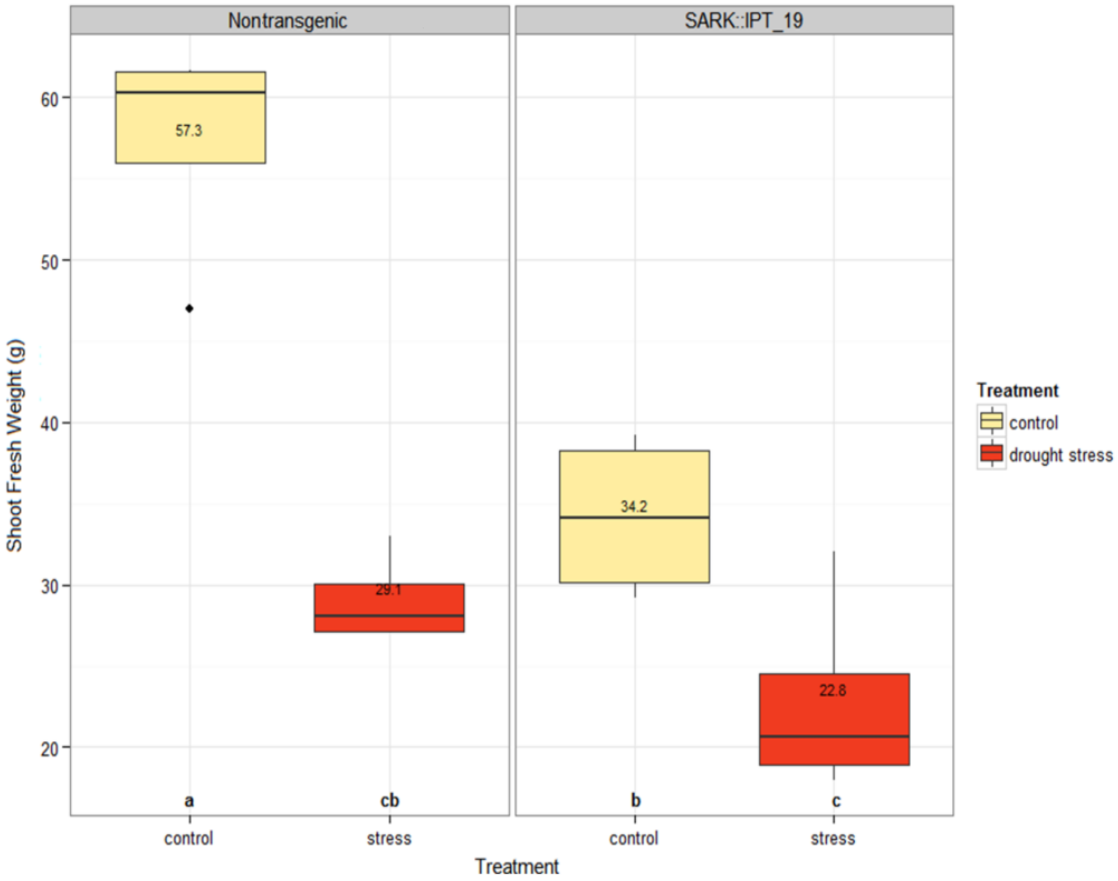

Figure 2.2. Shoot fresh weights of nontransgenic and *SARK::IPT* plants after drought stress test. Left panel shows nontransgenic plants, right panel shows *SARK::IPT* plants. Lower case letters indicate statistically significant group differences according to Tukey's HSD test.

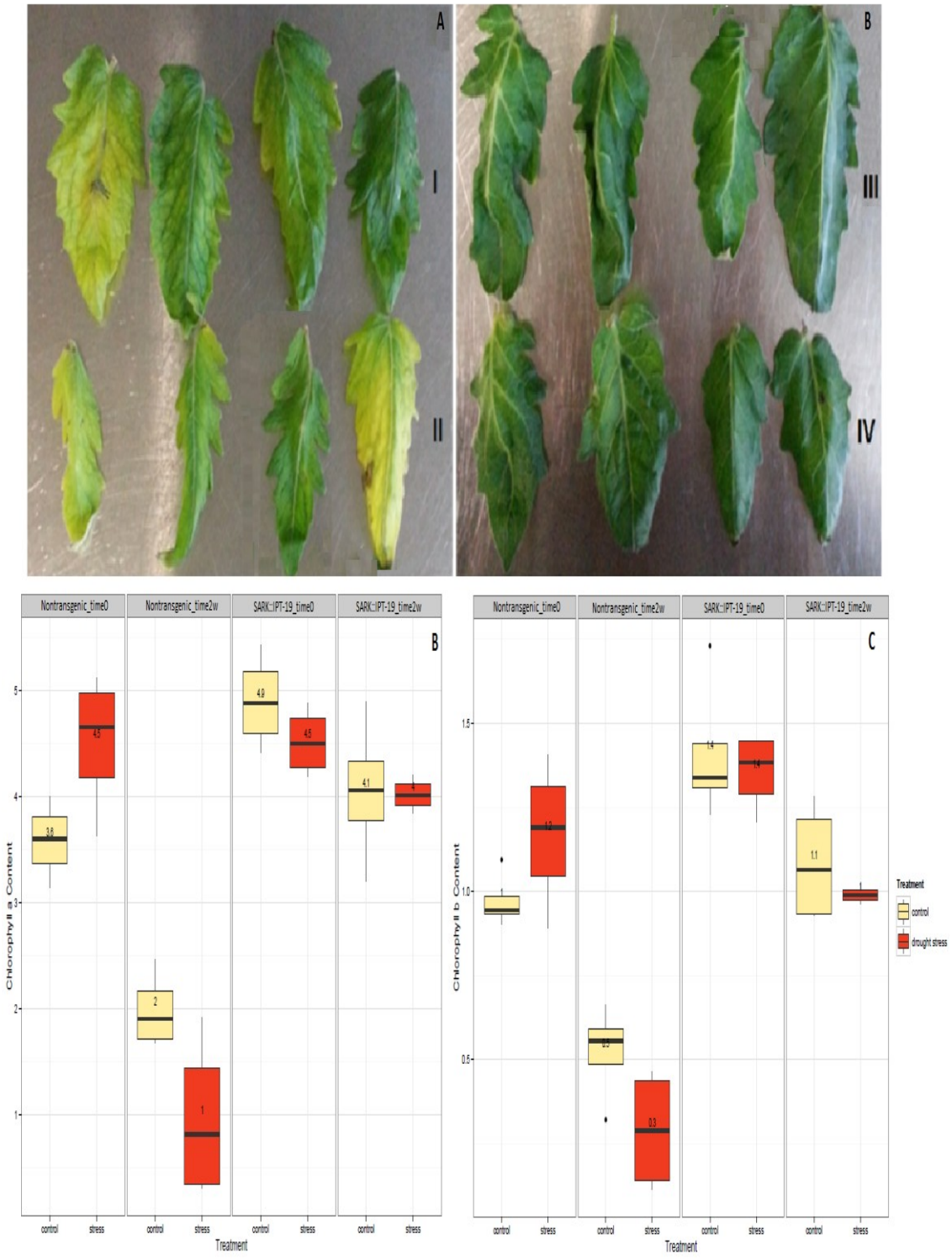

Figure 2.3. Detached leaf senescence assay results for nontransgenic and *SARK::IPT* plants grown under control and drought stress conditions. In A: leaves in row I are from nontransgenic control, row II are from nontransgenicdrought stress, row III are from *SARK::IPT* control and row IV are from *SARK::IPT* drought stress plants. In B: left panel shows the chlorophyll contents of the nontransgenicplants, right panel shows the chlorophyll contents of the *SARK::IPT* plants. Lower case letters indicate statistically significant group differences according to Tukey's HSD test.

2.3.3. Shoot Fresh Weight, Relative Water Use Efficiency and MDA Measurements

The amount of water used by the plants was measured during the drought tests and used to calculate the relative water use efficiency (RWUE) as fresh weight (g)/water usage (kg). We observed a decrease in RWUE under drought stress conditions in both nontransgenic (33%) and *SARK::IPT* (13%) lines, but the nontransgenicline had a significantly higher reduction compared to the *SARK::IPT* line (Figure 2.4). A comparatively smaller decrease in RWUE in the *SARK::IPT* line suggests that the transgenic line had better water use efficiency under drought stress conditions. We also measured shoot fresh weight (FW) under control and drought stress conditions. We observed that the *SARK::IPT* plantwas 40% lighter than the nontrangenic control plant under control conditions. FW was reduced by drought stress in both nontransgenic and *SARK::IPT* plants, but there was a relatively smaller decrease in FW of the *SARK::IPT* transgenic plants (33% reduction in FW in *SARK::IPT* versus 49% reduction in FW in nontransgenicline) under drought stress conditions. This result also suggested that the CK expressing line was better adapted to drought stress.

At the end of the drought test, we measured MDA content, which is a measure of lipid peroxidation. We observed lower MDA levels in *SARK::IPT* compared to nontransgenic leaves in both control and drought stress conditions (Figure 2.4). Under drought stress conditions, the MDA levels increased around 1.5 fold both in nontransgenic and *SARK::IPT* lines compared to control conditions. Although an increase was observed in MDA content in both nontransgenic and *SARK::IPT* leaves under drought stress conditions, the nontransgenic line exhibited a higher level of MDA accumulation under drought stress conditions (1.8 fold higher than *SARK::IPT*), which wasa sign of elevated oxidative stress on lipid membranes. Under control conditions the nontransgenic line also accumulated significantly higher levels of MDA compared to *SARK::IPT* (around 1.8 fold). Lower MDA levels in *SARK::IPT* under both control and stress conditions compared to nontransgenic plants could be an indicator of a more effective antioxidant system.

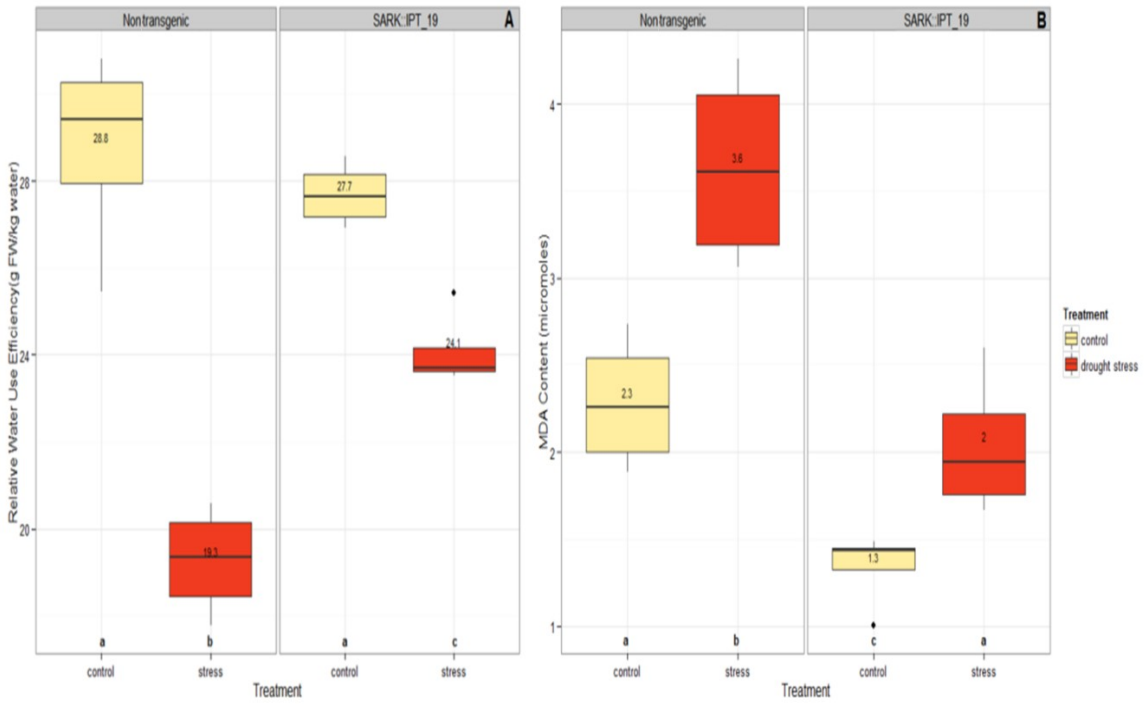

Figure 2.4. Relative water use efficiency and MDA content results of the nontransgenic and *SARK::IPT* plants grown under control and drought stress conditions. Lower case letters indicate statistically significant group differences according to Tukey's HSD test.

2.3.4. Selected Metabolite Analysis

We measured the levels of selected metabolites including amino acids (proline, glutamine, leucine, lysine, tryptophan, tyrosine; phenylalanine, valine, glutamate, arginine, asparagine, alanine, glycine, serine, threonine, methionine) organic acids (citric acid, lactic acid, pyruvic acid, malic acid, palmitic acid) and some major fatty acids (palmitoleic acid, stearic acid and linoleic acid) from the leaves of both nontransgenic and *SARK::IPT* lines grown under control and drought stress condition.

Amino acid measurements were conducted with a LC-MS/MS based method. We detected and collected data for 15 of the 20 proteogenic amino acids. We could not detect parent ions or fragmentation transitions in MS/MS analysis for five proteogenic amino acids (glycine, cysteine, isoleucine, tyrosine and histidine). Significantly lower levels of proline, asparagine, glutamine, leucine, lysine, phenylalanine, tryptophan, valine, aspartic acid, serine and threonine were observed in *SARK::IPT* compared to nontransgenic plants under normal growth conditions. Although a slight decrease was

observed in arginine, glutamic acid and aspartic acid levels in *SARK::IPT* compared to nontransgenic under control conditions, it was not statistically significant. For most (11 of 15) of the measured amino acids (proline, arginine, asparagine, glutamine, glutamic acid, leucine, lysine, phenylalanine, tryptophan, valine and aspartic acid) a significant increase in levels occurred under drought stress conditions in both the *SARK::IPT* and nontransgenic lines (Figure 2.5). Levels of serine and threonine also significantly increased under drought stress in *SARK::IPT* but no significant change was observed in the nontransgenic line. Levels of alanine decreased under drought stress conditions both in *SARK::IPT* and nontransgenic lines. No significant change was observed for methionine levels in both *SARK::IPT* and nontransgenic lines under control and drought stress conditions. Levels of proline, arginine, asparagine, glutamine, glutamic acid, leucine, lysine, phenylalanine, tryptophan, valine, serine, threonine and methionine were slightly lower in *SARK::IPT* compared to nontransgenic plants under drought stress conditions but this difference was not statistically significant. Levels of glutathione disulfide (GSSG), which is a conjugate of two glutathione molecules, were significantly increased under drought stress conditions in both *SARK::IPT* and nontransgenic lines. *SARK::IPT* had slightly lower levels of GSSG compared to the nontransgenic line under both control and drought stress conditions without statistical significance.

For organic acids, malic acid, citric acid and pyruvic acid levels increased under drought stress conditions in both the *SARK::IPT* and nontransgenic lines (Figure 2.5). Although a slight but not statistically significant increase was observed in lactic acid levels in the nontransgenic line, a significant increase was observed in the *SARK::IPT* line under drought stress conditions. *SARK::IPT* accumulated higher levels of malic acid under both control and drought stress conditions compared to nontransgenic. No significant difference was observed for citric acid levels in *SARK::IPT* compared to the nontransgenic line under control conditions but significantly lower citric acid levels were detected in *SARK::IPT* compared to the nontransgenic line under stress conditions. *SARK::IPT* plants accumulated significantly lower amounts of pyruvic acid and lactic acid under both control and drought stress conditions compared to the nontransgenic line.

We measured linoleic, palmitic, palmitoleic, heptadecanoic and stearic acid contents from the leaf tissues of *SARK::IPT* and nontransgenic lines grown under

control and drought stress conditions. For linoleic acid a significant increase was observed in both *SARK::IPT* and nontransgenic lines under drought stress conditions (Figure 2.5). No significant difference was observed between the *SARK::IPT* and nontransgenic lines for linoleic and palmitic acids under both control and drought stress conditions. Palmitoleic acid levels were significantly increased in *SARK::IPT* under drought stress, moreover its levels were significantly higher in *SARK::IPT* compared tothe nontransgenic line under drought stress conditions. For heptadecanoic acid, a significant increase was observed in *SARK::IPT* under drought stress but no change was observed in the nontransgenic line. Morever heptadecanoic acid levels in *SARK::IPT* plants were significantly lower compared to the nontransgenic line under control conditions but no significant difference was observed under stress conditions. No significant difference was observed between the *SARK::IPT* and nontransgenic line for stearic acid under both control and drought stress conditions.

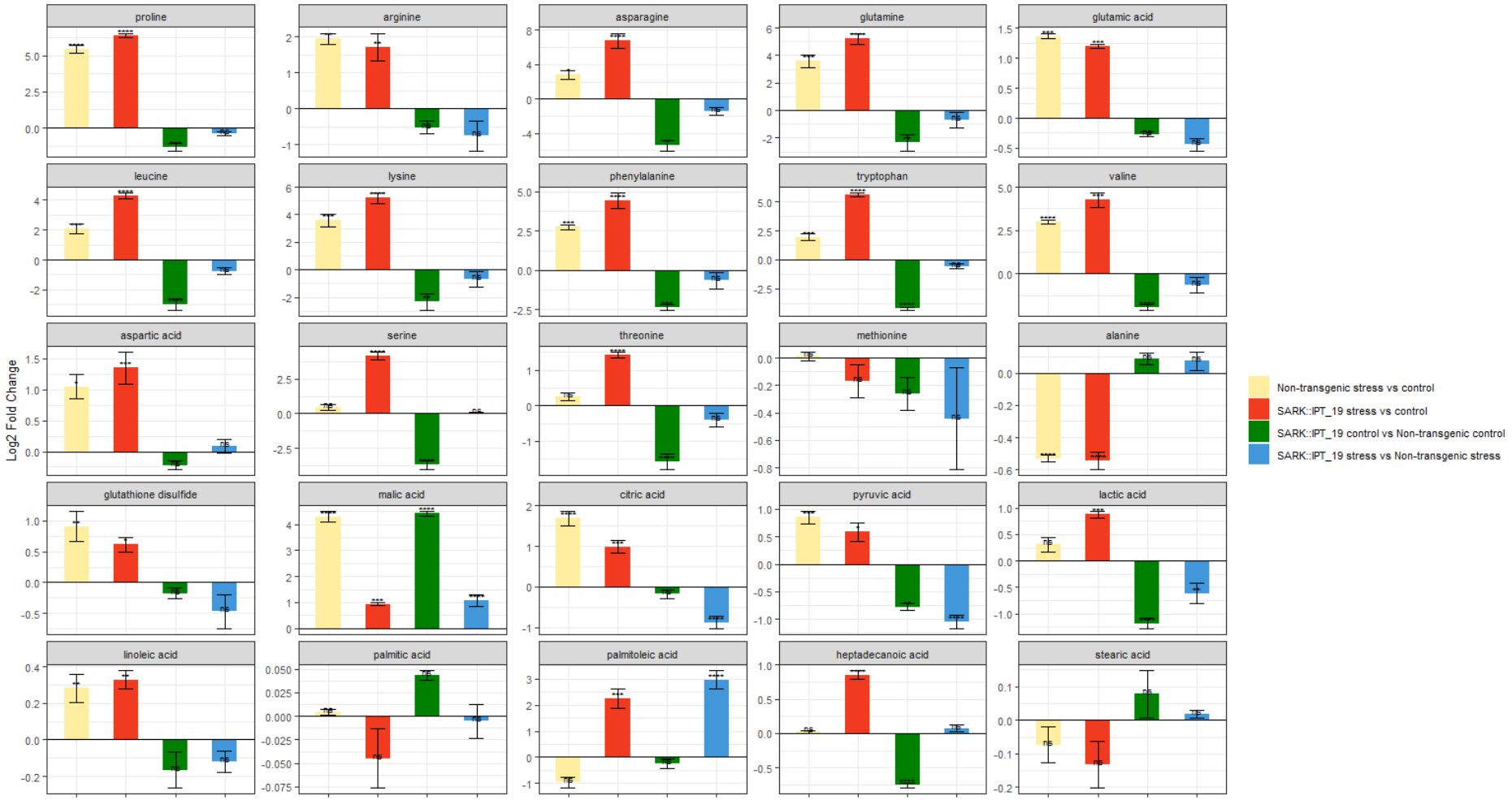

Figure 2.5. Selected metabolite content results for the nontransgenic and *SARK::IPT* plants grown under control and drought conditions. Log2 fold change in levels of amino acids (proline, arginine, asparagines, glutamine, glutate, leucin, lysine, phenylalanine, tryptophan, valine, aspartate, serine, threonine); organic acids (malic, citric, pyruvic and lactic acids); and fatty acids (linoleic, palmitic, palmitoleic, heptadecanoic, and steraic acids) are represented in boxplots. Asterisks indicate significantdifferences according to Tukey's HSD test

2.3.5. Proteome Analysis

We conducted proteomics analysis in transgenic (*SARK::IPT*) and nontransgenic MM control plants grown under control and drought stress conditions for understanding drought stress response mechanisms. A total of 1714 proteins were identified with FDR<1%, corresponding to more than 5400 unique peptide sequences in the leaf total protein samples. To identify proteins that were differentially abundant in response to drought stress, we used a spectral counting-based analysis that estimates protein amount from the number of assigned MS/MS spectra and an MRM-based quantitation of selected identified peptides. Target peptide selection for MRM analysis was carried out by selecting the differentially abundant proteins in the initial untargeted LC/MS-MS analysis and the proteins which were known to be related to drought or CK responses. In this way from the targeted proteomic data acquired by MRM analysis, 207 proteins were found to be significantly differentially abundant in the nontransgenic or *SARK::IPT* plants under drought versus control conditions. Of these, 71 proteins (34%) were differentially regulated both in nontransgenic and *SARK::IPT* plants, whereas 109 (53%) were identified to be differentially abundant just in *SARK::IPT* plants and 27 (13%) were identified to be differentially abundant in nontransgenic plants under drought stress conditions (Figure 2.6).

For the leaf nuclear enriched proteome, a total of 1199 proteins were identified with FDR<1%, corresponding to more than 3360 unique peptide sequences in the leaf nuclear enriched extracts. Of these 3360 peptides, 2206 (65.7%) were shared with leaf total proteome extracts and 1154 (34.3%) peptides were unique to nuclear enriched extracts. From the identified 1199 proteins, 883 (73.6%) were shared with the leaf total proteome extract and 316 (26.4%) were unique to nuclear enriched extracts. We used the UniProt (http://www.uniprot.org/) and PANTHER (http://www.pantherdb.org/) databases to find the locations of the proteins. If the relevant information was not found in these databases, we searched the TAIR database (https://www.arabidopsis.org/) for *Arabidopsis* homologs of the tomato proteins. We selected potentially nuclear-localized proteins as candidates for further quantification in MRM analysis. In this way, 81 proteins were found to be differentially abundant in the nontransgenicor *SARK::IPT* plants under drought versus control conditions. Around one third of drought-responsive

proteins (38%, 31 proteins out of 81) that were differentially abundant in nontransgenic plants were also differentially abundant in *SARK::IPT* plants, whereas 31 proteins (38%) were only differentially regulated in *SARK::IPT*plants and 19 (24%) were only differentially abundant in nontransgenic plants (Figure 2.8).

2.3.5.1. Functional Annotation and Classification of the Differentially Represented Proteins

Functional GO term annotation and classification of our datasets were conducted based on PANTHER and Uniprot database analysis. PANTHER Go-Slim biological function analysis of the 180 and 98 differentially regulated proteins from the total leaf proteome of *SARK::IPT* and nontransgenic plants, respectively, indicated that 166 (92.2%) and 84 (85.7%) proteins could be assigned to a given function, respectively (Figure 2.6). In both *SARK::IPT* and nontransgenic lines, the majority of differentially abundant proteins were associated with metabolic and cellular processes with 65 (37.4%) proteins for metabolic and 54 (31%) proteins for cellular processes for *SARK::IPT* plants and 32 (33.7%) proteins for both metabolic and cellular processes for nontransgenic lines. Other important categories were response to stimulus and biological regulation for the *SARK::IPT* line with 21 (12.1%) and 10 (5.7%) proteins each. The same categories were the third and fourth most important categories for nontransgenicplants with 7 (7.4%) and 6 (6.3%) proteins, respectively. In functional grouping based on MAPMAN categories, the largest protein groups were related to photosynthesis (23 proteins, 12.8%), protein metabolism (22 proteins, 12.2%), redox (19 proteins, 10.5%) and stress (10 proteins, 5.6%) in the *SARK::IPT* line (Figure 2.6). In the nontransgenic line, the largest protein groups based on MAPMAN categories were protein metabolism (16 proteins, 16.3%), photosynthesis and redox with (7 proteins each, 7.1%), and amino acid metabolism and RNA metabolism (6 proteins each, 6.1%).

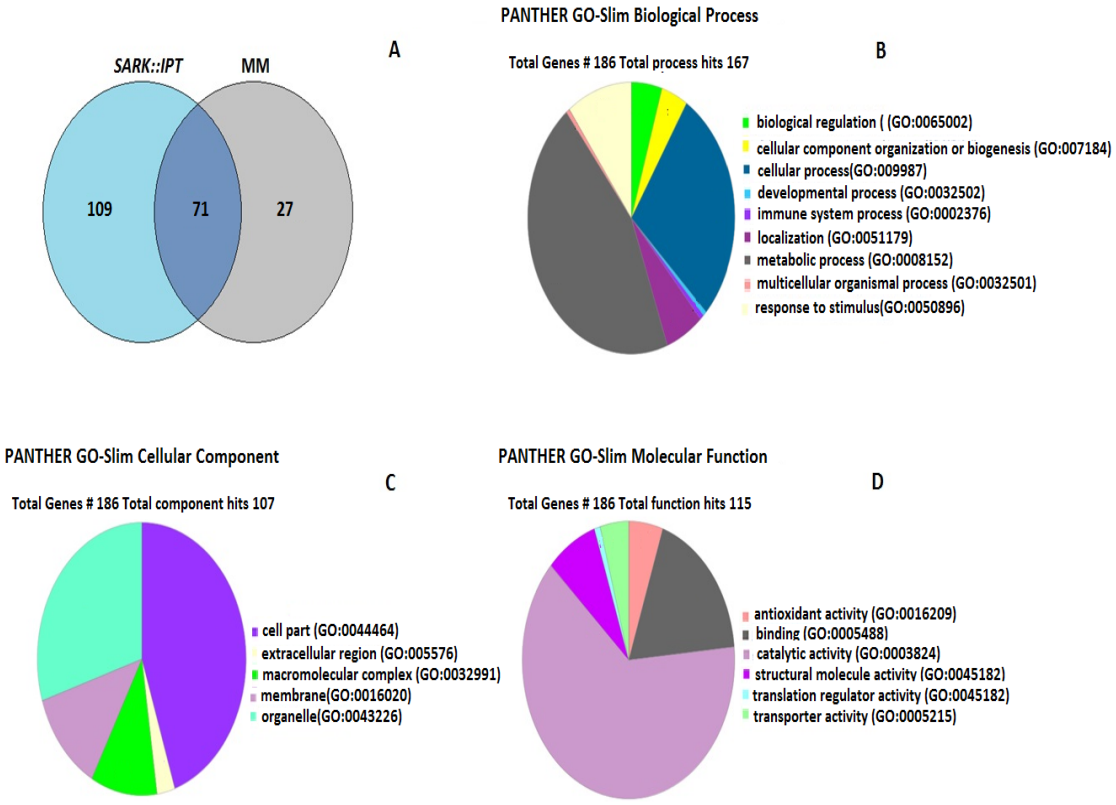

Figure 2.6. Functional classification of differentially abundant proteins in the total leaf proteome dataset. A: Differentially abundant proteins in transgenic and nontransgenic plants under drought stress compared to control. B: Functional classification of differentially represented proteins based on PANTHER GO-Slim biological processes in *SARK::IPT* and nontransgenic plants under drought stress. C: Functional classification of differentially represented proteins based on PANTHER GO-Slim molecular function in *SARK::IPT* and nontransgenic plants under drought stress. D: Functional classification of differentially represented proteins based on PANTHER GO-Slim cellular component in *SARK::IPT* and nontransgenic plants under drought stress.

Based on PANTHER analysis from the *SARK::IPT* line, a total of 113 (62.8%) and 51 (52.0%) differentially abundant proteins from the nontransgenic line were assigned to GO-Slim molecular functions with the majority, 65 (37.4%) and 28 (29.5%) proteins, having catalytic activity in the *SARK::IPT* and nontransgenic lines, respectively (Figure 2.6). Other proteins had binding [23 (13.2%) for *SARK::IPT* and 13 (13.7%) for nontransgenic lines], antioxidant [13 (7.5%) for *SARK::IPT* and 4 (4.2%) for nontransgenic lines] and structural molecule [8 (4.6%) for *SARK::IPT* and 5 (5.3%) for nontransgenic lines] activities. A total of 105 (58.3%) and 64 (65.3%) differentially abundant proteins were associated with GO-Slim cellular component categories for the *SARK::IPT* and nontransgenic lines, respectively (Figure 2.6). Most were assigned to the cell [53(30.5%) for *SARK::IPT* and 32 (33.7%) for nontransgenic lines] and

organelles [31 (17.8%) for *SARK::IPT* and 18 (18.9%) for nontransgenic lines] and macromolecular complex [12 (6.9%) for *SARK::IPT* and 7 (7.4%) for nontransgenic lines].

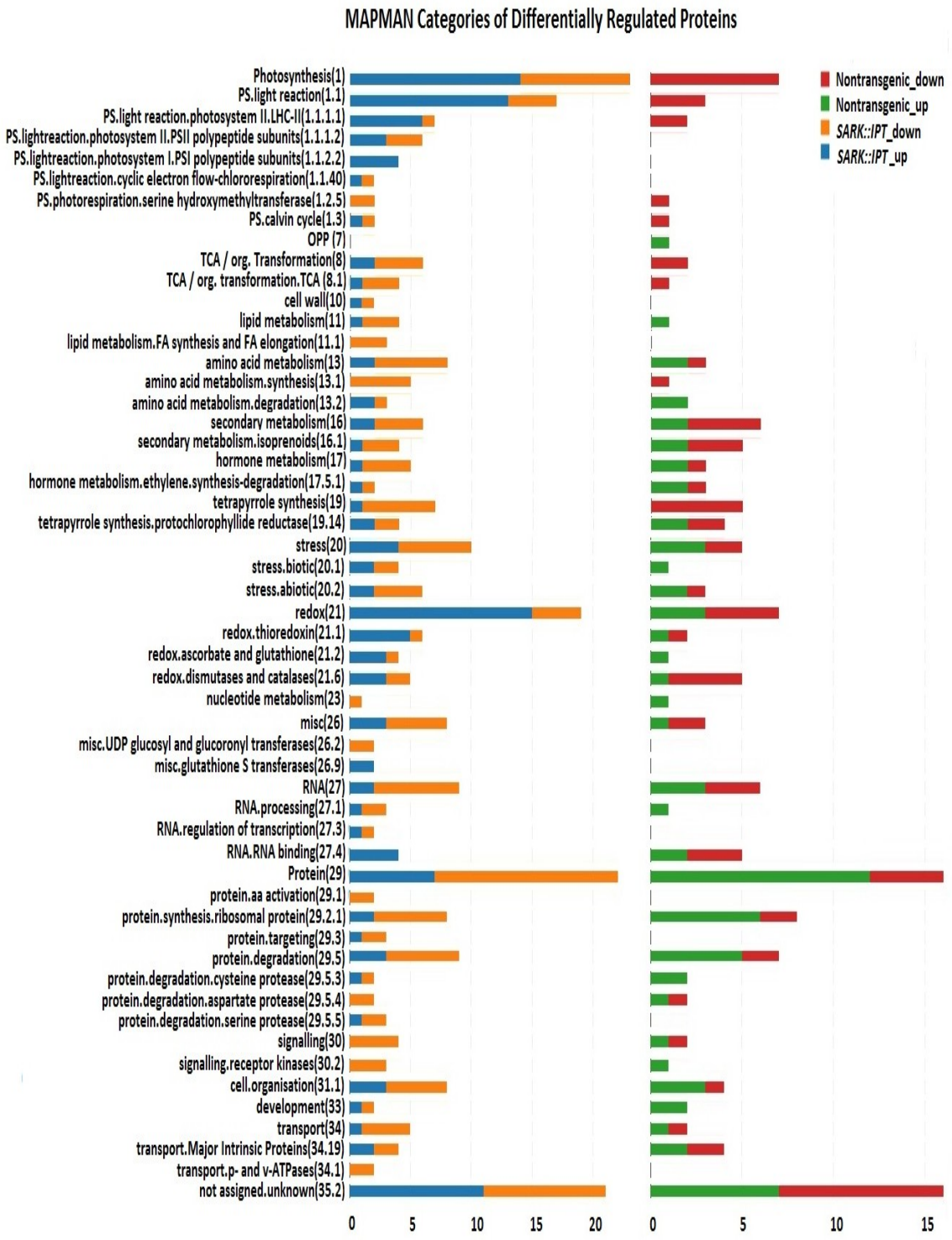

Figure 2.7. MAPMAN functional categories of differentially abundant proteins in total leaf proteome dataset. *SARK::IPT* line data are on the left side, nontransgenic line data are on the right side of the figure.

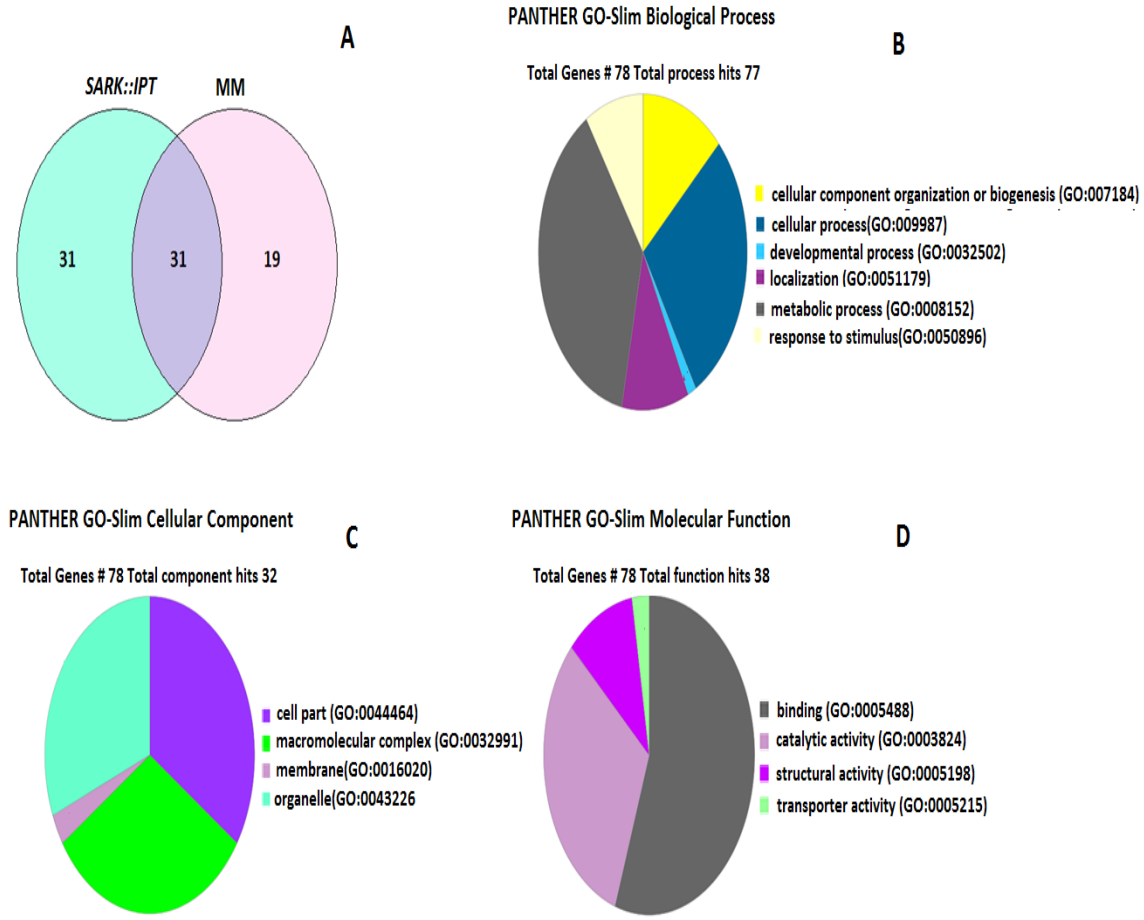

Figure 2.8. Functional classification of differentially represented proteins in leaf nuclear enriched proteome dataset. A: shows differentially abundant proteins in *SARK::IPT* and nontransgenic plants under drought stress condition compared to control condition. B: Functional classification of differentially represented proteins based on PANTHER GO-Slim biological processes. C: Functional classification of differentially represented proteins based on PANTHER GO-Slim cellular components. D: Functional classification of differentially represented proteins based on PANTHER GO-Slim molecular functions.

Nearly all (98.7%) of the 68 differentially regulated proteins from the nuclear proteome were assigned biological function based on PANTHER GO-Slim analysis. Similar to the total proteome, the most numerous categories were metabolic (29 proteins, 36%) and cellular (22 proteins, 29%) processes (Figure 2.8). Significant numbers of proteins were also associated with cellular component organization, localization and response to stimulus. In manual grouping based on GO term annotation and MAPMAN categories, the largest protein groups were related to RNA binding and processing (18 proteins, 26.5%), protein metabolism (16 proteins, 23.5%) and transcription factors (15 proteins, 22.0%). Only 48.7% of the nuclear proteins were

assigned a molecular function based on PANTHER GO-Slim analysis (Figure 2.8). More than half (21 proteins) had binding activity with fewer proteins assigned to catalytic and structural molecule activity in PANTHER analysis. Approximately 81% of the proteins were assigned specific molecular functions including 21 (55%) as nucleic acid binding proteins (Figure 2.8).

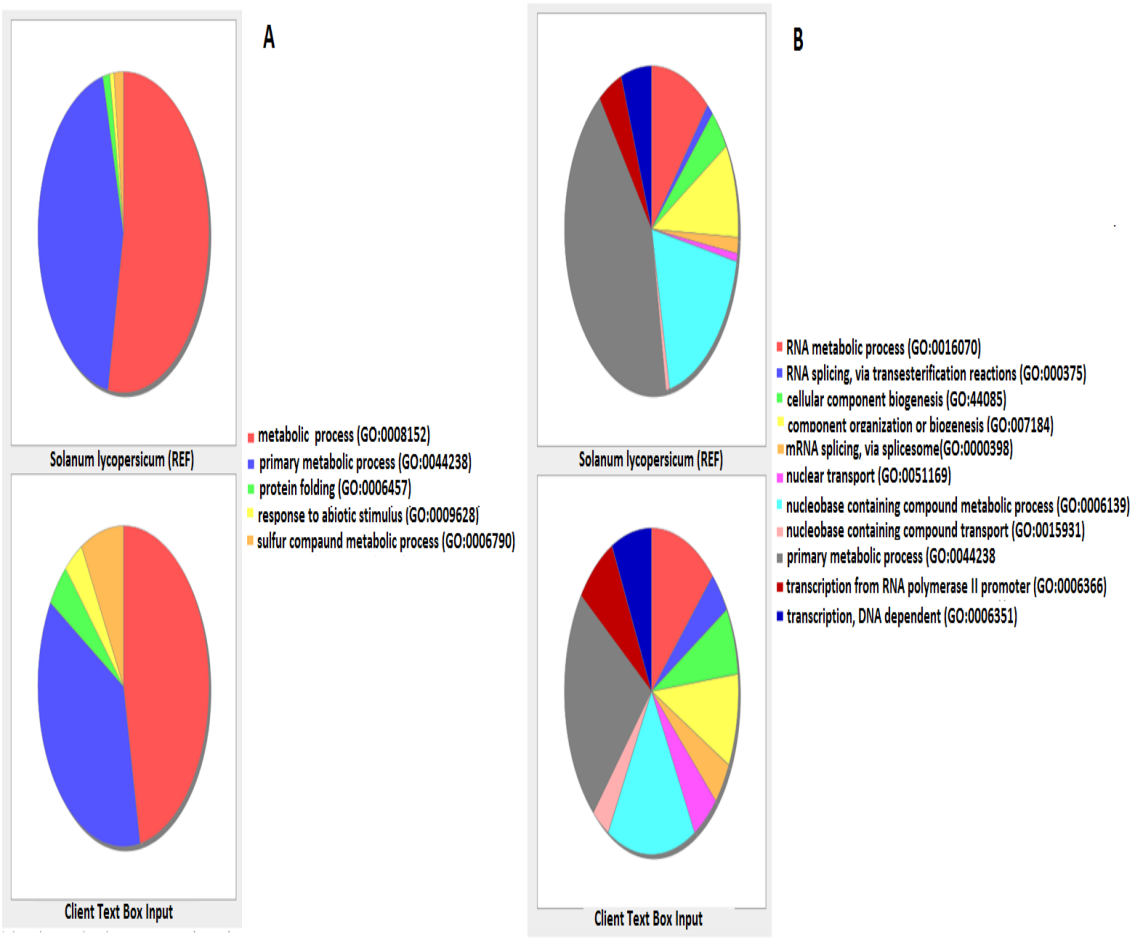

Figure 2.9. PANTHER over-representation results based PANTHER GO-Slim biological processes categorization. A: PANTHER over-representation results for leaf total proteome dataset. B: PANTHER over-representation results for leaf nuclear enriched proteome dataset.

A functional over-representation test was conducted for understanding which group(s) of proteins were most abundant in our datasets. According to this analysis, the total leaf proteome was enriched in proteins related to the biological processes: sulfur compound metabolism (mainly thioredoxin protein), response to abiotic stimulus, protein folding and primary metabolism at 9, 9, 6.5 and 1.7 fold, respectively (Figure 2.9). In a more detailed over-representation analysis based on complete GO biological

processes, enriched proteins were related to chlorophyll biosynthetic process (100 fold), isopentenyl diphosphate biosynthetic process (64 fold), glycerol ether metabolic process (41 fold), pentose-phosphate shunt (36 fold), photosynthesis, light harvesting (29 fold), cellular response to oxidative stress (26 fold) and protein-chromophore linkage (19 fold).

The differentially represented nuclear proteome data were also analysed for PANTHER over-representation. As a result, proteins related to nuclear transport (22.5 fold), RNA splicing, via transesterification reactions (12 fold) and transcription from RNA polymerase II promoter (6 fold) were found to be enriched in our nuclear proteome data (Figure 2.9).

2.3.5.2. MAPMAN Cluster Analysis of Proteomics Data

MAPMAN annotation was conducted for the acquired leaf total and leaf nuclear enriched proteomic datasets for proteins with differential abundance in *SARK::IPT* and nontransgenic lines under control versus drought conditions. Cluster analysis was conducted to visualize the expression patterns of the identified proteins for the different tested lines. The different test groups were the expression level changes between *SARK::IPT* control versus drought stress data and the nontransgenic control versus drought stress data. The clustering analysis groups proteins with similar expression patterns in the different test groups into a cluster. Clustering patterns can be useful to infer information about different protein groups that may have roles in regulation of the CK effect on drought stress response. Leaf total proteomics data were grouped into four clusters based on expression patterns in the different test groups (Figure 2.10).

For the leaf total proteome data, clusters 1 and 2 were composed of proteins which had increased levels in the *SARK::IPT* line under drought stress conditions, whereas the levels of the same proteins of the nontransgenic line were increased, unchanged or decreased under drought stress conditions. Cluster 1 consisted of 54 proteins which were upregulated in the *SARK::IPT* line under drought stress, whereas a slight increase, a slight decrease or no change was observed in the nontransgenic line. Of these 54 proteins, 49 were significantly upregulated by drought stress in the

transgenic line, just 11 proteins were significantly differentially regulated by drought stress in the nontransgenic line (please see Appendix Table A.3). The MAPMAN categories in cluster 1 were photosynthesis with 15 proteins, protein metabolism with 5 proteins, thioredoxins with 4 proteins, peroxiredoxin with 3 proteins, dismutase and catalase with 2 proteins, ascorbate glutathione with 2 proteins, glutathione S transferase with 2 proteins, RNA with 2 proteins, TCA with 2 proteins, cell organization with 2proteins and stress with 2 proteins. Proteins in cluster 1 exhibited most different response to drought stress in *SARK::IPT* compared to nontransgenic line. Cluster 2 consisted of 8 proteins, which had increased levels in both *SARK::IPT* and nontransgenic plants in response to drought stresss (please see Appendix Table A.3). MAPMAN categories in cluster 2 were diverse with proteins having roles in lipid metabolism, secondary metabolism, redox, RNA, and transport. Proteins in cluster 2 exhibited a similar response to drought stress in *SARK::IPT* compared to nontransgenic line, whereas the upregulation levels were lower in nontransgic line.

Clusters 3 and 4 consisted of proteins, which had slightly less downregulation or slightly higher upregulation of stress responsive proteins in thenontransgenicline compared to the *SARK::IPT* line. Cluster 3 contained 115 proteins which had reduced levels in *SARK::IPT* under drought stress conditions but were reduced, not changed or slightly increased in the nontransgenic line under drought stress condition. Of these 115 proteins, 110 of them were downregulated in the *SARK::IPT* line under drought stress, whereas 59 of them were downregulated or slightly upregulated in the nontransgenic line under drought stress (please see Appendix Table A.3). The MAPMAN categories in cluster 3 were protein metabolism with 16 proteins, photosynthesis with 9 proteins, RNA with 8 proteins, amino acid metabolism with 7 proteins, tetrapyrrole biosynthesis with 7 proteins, stress with 7 proteins, cellular processes with 7 proteins, hormone metabolism with 5 proteins, signalling with 5 proteins, TCA with 4 proteins, secondary metabolism with 4 proteins, redox with 4 proteins, transport with 4 proteins and lipid metabolism with 3 proteins. Cluster 4 consisted of 33 proteins which were downregulated, not changed or slightly upregulated in the *SARK::IPT* line under drought stress, whereas proteins in this cluster were upregulated in the non-trangenic line under drought stress. Of these 33 proteins, 24 were slightly downregulated or upregulated in the *SARK::IPT* line under stress, while 32 of them were upregulated in the nontransgenic under drought stress (please see Appendix Table A.3). The most abundant MAPMAN categories in cluster 3 were protein metabolism with 8 proteins,

cellular processes with 3 proteins, stress with 3 proteins, hormone metbabolism with 2 proteins, redox with 2 proteins and rest of them beloged to diverse categories. Proteins in cluster 4 exhibited a similar response to drought stress in the *SARK::IPT* line compared to the nontransgenic line, with higher upregulation observed in the nontransgenic line.

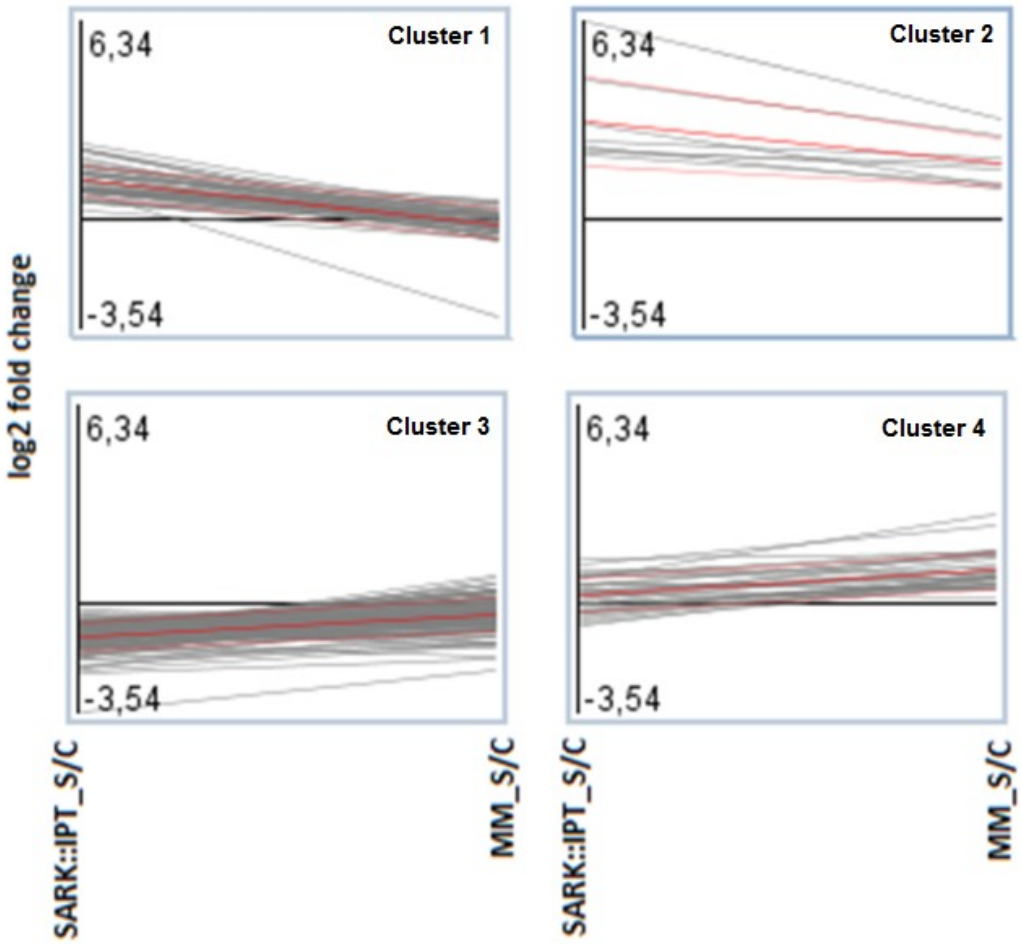

Figure 2.10. MAPMAN cluster analysis results of leaf total proteins differentially abundant between test groups

We also conducted MAPMAN cluster analysis for the leaf nuclear enriched proteomic dataset. The leaf nuclear enriched proteomic dataset was separated into 4 clusters for the proteins which were differentially abundant in transgenic and nontransgenic plants under drought stress condition (Figure 2.11).

Cluster 1 of the nuclear enriched data contained proteins which were upregulated or not changed under drought stress in the *SARK::IPT* line, but downregulated in nontransgenic plants under drought stress. Cluster 1 consisted of 31 proteins. Of these

31 proteins, 22 were upregulated in the *SARK::IPT* line under drought stress, whereas 26 were downregulated in the nontransgenic line under drought stress conditions (please see Appendix Table A.4). The MAPMAN categories in cluster 1 were RNA with 10 proteins, DNA with 3 proteins, protein with 7 proteins, development with 2 proteins and the rest are from diverse groups. Cluster 1 contained very interesting proteins which are upregulated in *SARK::IPT* but downregulated in the nontransgenic line, which indicates that they may contribute to the drought response difference of the two lines. Proteins in cluster 1 exhibited the most different response to drought stress in *SARK::IPT* compared to the nontransgenic line.

Cluster 2 contained proteins which are upregulated in both the *SARK::IPT* and nontransgenic lines in response to drought. Cluster 2 consisted of 20 proteins. Of these 20 proteins, 18 of them were significantly upregulated in the *SARK::IPT* line, whereas 8 proteins were significantly upregulated in the nontransgenic line under drought stress (please see Appendix Table A.4). The MAPMAN categories in cluster 2 were RNA with 4 proteins, protein with 3 proteins, DNA with 2 proteins, stress with 2 proteins and and the rest are from diverse groups. Proteins in cluster 2 exhibited similar response to drought stress in both *SARK::IPT*and nontransgenic lines.

Cluster 3 contained proteins which were downregulated in the *SARK::IPT* line under drought stress, but upregulated or not changed in the nontransgenic line. Cluster 3 contained 14 proteins. Of these 14 proteins, 13 of them were downregulated in the *SARK::IPT* line under drought stress, but 8 proteins were upregulated in the nontransgenic line under drought stress (please see Appendix Table A.4). The MAPMAN categories in cluster 3 were RNA regulation of transcription with 5 proteins, RNA binding with 3 proteins, protein degradion with 2 proteins and protein posttranslational modification with 2 proteins. Proteins in cluster 3 also exhibited a diffent response to drought stress in *SARK::IPT* plants compared to nontransgenic line.

Cluster 4 contained proteins which were downregulated in both the *SARK::IPT* and nontransgenic lines under drought stress, with a stronger downregulation observed in the nontransgenic line. Cluster 4 contained 12 proteins. Of these, 12 proteins 5 were downregulated in the *SARK::IPT* line under drought stress and all of them were downregulated under drought stress in the nontransgenic line (please see Appendix Table A.4). The MAPMAN categories in cluster 4 were RNA processing with 4 proteins, RNA regulation of transcription with 2 proteins, DNA synthesis with 2 proteins, and protein degradation with 3 proteins. Proteins in cluster 4 also exhibited a

similar response to drought stress in *SARK::IPT*compared to the nontransgenic line, however, a stronger repression was observed in the nontransgenic line for those proteins under drought stress response.

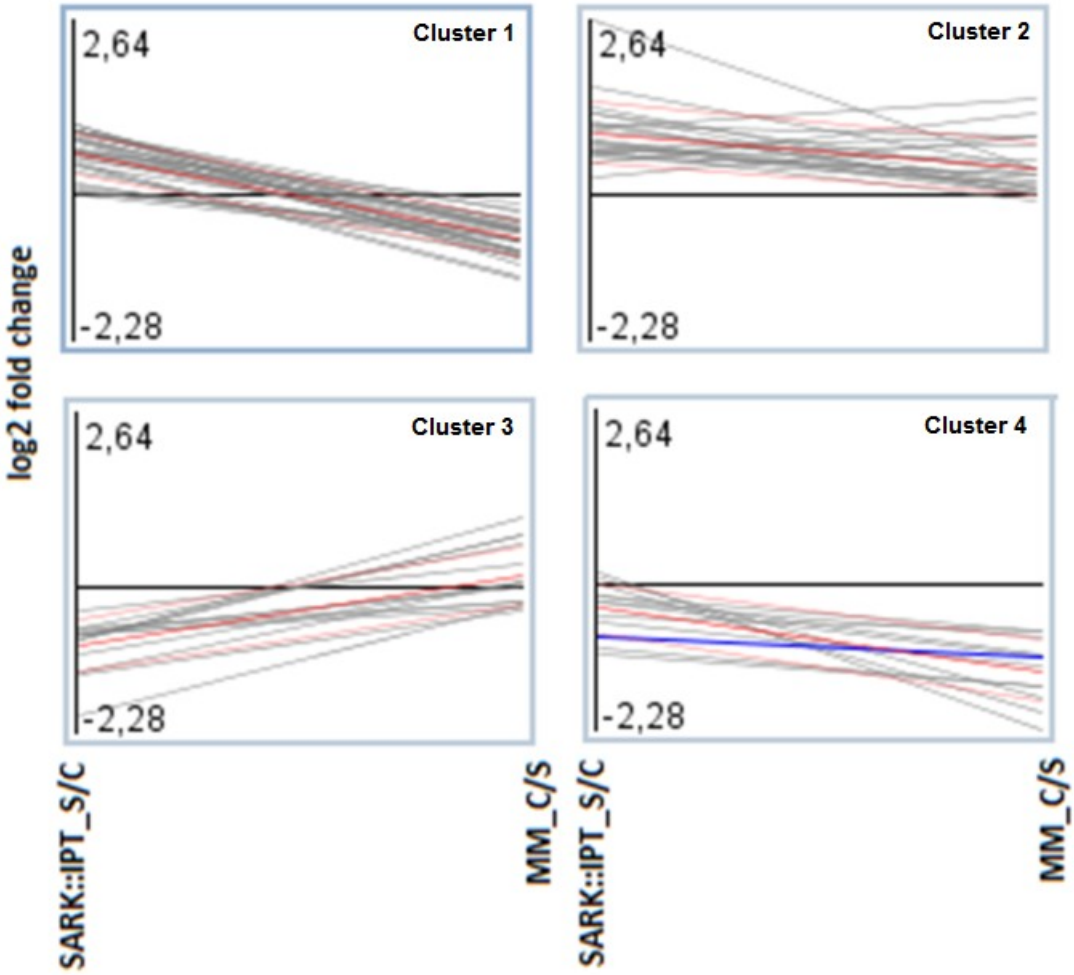

Figure 2.11. MAPMAN cluster analysis results of leaf nuclear enriched proteins that were differentially abundant between test groups

The 10 most strongly overexpressed and downregulated proteins from the *SARK::IPT* leaf total proteome dataset under drought stress are listed in Table 2.1. Of the 10 most strongly upregulated proteins, ASR4, beta-tonoplast intrinsic protein, REF-like stress related protein, thioredoxin and non-specific lipid-transfer protein are known to be stress inducible or ABA responsive proteins, which could have roles in the drought stress response and tolerance (Golan et al., 2014; Mao et al., 2015; Kim et al., 2016; Ueoka-Nakanishi et al., 2013; Liu et al., 2015),. Unexpectedly,the chloroplastic proteins thylakoid lumenal 19 kDa protein, chlorophyll a-b binding protein and oxygen-evolving enhancer protein 3, which have roles in photosynthesis or maintainance of photosynthetic machinery were also strongly upregulated in *SARK::IPT* plants. This

result could be related to regulation of the photosynthetic machinery by increased CK levels. Of the 10 most strongly downregulated proteins, 4 proteins related to protochlorophyllide reductase, magnesium-protoporphyrin IX monomethyl ester (oxidative) cyclise, protochlorophyllide reductase like protein and geranylgeranyl reductase are known to be involved in chlorophyll biosynthesis. Strong downregulation of chlorophyll biosynthetic enzymes could be an indicator of stress in the *SARK::IPT* lines.

Table 2.1. List of the 10 most strongly overexpressed and 10 most strongly downregulated proteins from leaf total proteome dataset in *SARK::IPT* line under drought stress

ID	Description	MAPMAN Category	Change	*SARK::IPTs/ SARK::IPTc*	Pval_ *SARK:: IPT*	MMs/ MMc	Pval _MM
Solyc03g019820.2.1	Aquaporin	transport.Major Intrinsic Proteins.TIP	+	6.3	7.5E-05	3.3	3.8E-06
Solyc10g075100.1.1	Non-specific lipid-transfer protein	lipid metabolism.lipid transfer proteins etc	+	4.5	3.3E-06	2.7	1.3E-03
Solyc07g064600.2.1	Endoribonuclease L-PSP family protein	RNA.processing.ribonucleases	+	3	1.0E-06	1.1	3.8E-02
Solyc04g071620.2.1	ASR4 (Fragment)	not assigned.unknown	+	2.5	5.2E-04	2	5.9E-05
Solyc01g087040.2.1	Thylakoid lumenal 19 kDa protein. chloroplastic	PS.lightreaction.photosystem II.PSII polypeptide subunits	+	2.4	1.8E-04	0.2	ns
Solyc04g080850.2.1	Thioredoxin	redox.thioredoxin	+	2.4	1.3E-02	1	2.7E-05
	REF-like stress related protein 1	secondary metabolism.isoprenoids	+	2.3	9.4E-04	1.6	2.0E-05
Solyc12g011280.1.1	Chlorophyll a-b binding protein 8. chloroplastic	PS.lightreaction.photosystem II.LHC-II	+	2.3	5.0E-08	0.2	ns
Solyc11g044530.1.1	PAP fibrillin	cell.organisation	+	2.3	1.7E-02	-0.6	9.1E-03
Solyc02g079950.2.1	Oxygen-evolving enhancer protein 3	PS.lightreaction.photosystem II.PSII polypeptide subunits	+	2.3	2.7E-06	-0.3	1.5E-02
Solyc12g013710.1.1	Protochlorophyllide reductase	tetrapyrrole synthesis.protochlorophyllide reductase	-	-3.5	4.0E-07	-2.2	7.2E-05
Solyc10g077040.1.1	Magnesium-protoporphyrin IX monomethyl ester	tetrapyrrole synthesis.magnesium-protoporphyrin IX monomethyl ester (oxidative) cyclase	-	-2.3	1.9E-05	-1.8	3.0E-08

(cont. on next page)

Table 2.1. (cont.)

ID	Description	MAPMAN Category	Change	*SARK::IPTs/ SARK::IPTc*	Pval_ *SARK:: IPT*	MMs/ MMc	Pval _MM
Solyc01g079940.2.1	Xylanase inhibitor (Fragment)	protein.degradation.aspartate protease	-	-2.2	6.5E-05	-1.4	4.0E-06
Solyc01g011480.1.1	Photosystem II CP43 chlorophyll apoprotein	PS.lightreaction.photosystem II.PSII polypeptide subunits	-	-2	1.6E-04	-0.3	ns
Solyc08g067030.2.1	Os01g0611000 protein (Fragment)	not assigned.unknown	-	-2	1.2E-07	-0.8	3.2E-04
Solyc03g005260.2.1	Sulfate adenylyltransferase	S-assimilation.ATPS	-	-2	2.0E-04	-1.2	1.2E-04
Solyc07g054210.2.1	Protochlorophyllide reductase like protein	tetrapyrrole synthesis.protochlorophyllide reductase	-	-1.8	4.8E-07	-1.4	5.4E-07
Solyc03g115980.1.1	Geranylgeranyl reductase	secondary metabolism.isoprenoids.non-mevalonate pathway	-	-1.8	1.1E-02	-1.1	2.2E-03
Solyc08g006890.2.1	Tubulin alpha-3 chain	cell.organisation	-	-1.7	7.6E-04	0	ns
Solyc10g086150.1.1	Single-stranded DNA binding protein	RNA.RNA binding	-	-1.7	2.9E-05	-0.7	7.1E-04

The 10 most strongly over-expressed and 10 most strongly downregulated proteins from the leaf nuclear enriched proteome dataset under stress are listed in Table 2.2. The strongly upregulated protein list contained two proteins with transcription factor function (transcriptional activator protein Pur-alpha, nascent polypeptide-associated complex, alpha subunit), one protein with DNA repair function (UV excision repair protein RAD23), a H1 histone-like protein and DNA helicase protein (holliday junction ATP-dependent DNA helicase ruvB), which could potentially affect chromatin structure and gene expression. The strongly downregulated protein list contained 4 proteins with transcription factor activity (BEL1-like homeodomain protein 1, CCAAT-box-binding transcription factor-like protein, Chromodomain-helicase-DNA-binding protein 6, Histone deacetylase 2a-like IPR007087 Zinc finger) and a ATP-dependent RNA helicase, which could potentially affect chromatin structure and gene expression.

Table 2.2. List of the10 most strongly overexpressed and 10 most strongly downregulated proteins from leaf nuclear enriched proteome dataset in *SARK::IPT* line under drought stress.

ID	Description	MAPMAN Category	Change	*SARK::IPTs/ SARK::IPTc*	Pval_*SARK::IPT*	MMs/ MMc	Pval _MM
Solyc04g082200.2.1	Dehydrin	not assigned.unknown	+	2.6	1.3E-04	0.38	ns
Solyc02g084240.2.1	H1 histone-like protein	DNA.synthesis/ chromatin structure.histone	+	1.6	2.6E-05	0.4	0.0E+00
Solyc04g009410.2.1	Senescence-associated protein DIN1	protein.degradation.ubiquitin.proteasom	+	1.3	5.1E-05	0.08	ns
Solyc01g049680.2.1	Transcriptional activator protein Pur-alpha	RNA.regulation of transcription.unclassified	+	1.2	5.1E-03	-0.04	ns
Solyc06g062350.2.1	Holliday junction ATP-dependent DNA helicase ruvB	development.unspecified	+	1.1	3.2E-08	-0.01	ns
Solyc11g068640.1.1	Os11g0175900 protein (Fragment)	not assigned.unknown	+	1.1	8.0E-05	0.09	ns
Solyc06g008150.2.1	Ulp1 peptidase-like	not assigned.unknown	+	1.1	1.7E-04	0.89	0.0E+00
Solyc01g009080.2.1	FHA domain containing protein	not assigned.unknown	+	1	2.1E-04	-1.08	0.0E+00
Solyc03g117780.2.1	UV excision repair protein RAD23	DNA.repair	+	1	1.9E-02	1.44	0.0E+00
Solyc10g081030.1.1	Nascent polypeptide-associated complex alpha subunit-like protein	protein.synthesis.elongation	+	1	7.8E-03	-0.56	0.0E+00
Solyc02g067210.2.1	Nucleic acid binding protein	RNA.RNA binding	-	-0.7	2.9E-04	-0.31	0.0E+00
Solyc02g064700.2.1	Protein serine_threonine kinase	protein.postranslational modification	-	-0.8	2.4E-04	0	ns
Solyc01g007070.2.1	BEL1-like homeodomain protein 1	RNA.regulation of transcription.HB,Homeobox transcription factor family	-	-0.8	ns	0.76	0.0E+00
Solyc12g014210.1.1	RNA binding protein	RNA.RNA binding	-	-0.8	7.1E-04	0.79	ns
Solyc03g123530.2.1	CCAAT-box-binding transcription factor-like protein	RNA.regulation of transcription.CCAAT box binding factor family, DR1	-	-0.9	2.1E-02	1.05	0.0E+00

(cont. on next page)

Table 2.2. (cont.)

ID	Description	MAPMAN Category	Change	*SARK::IPTs/ SARK::IPTc*	Pval_*SARK::IPT*	MMs/ MMc	Pval _MM
Solyc03g114370.2.1	Atp-dependent RNA helicase	DNA.synthesis/ chromatin structure	-	-1	2.4E-03	-1.61	0.0E+00
Solyc02g014770.2.1	Chromodomain-helicase-DNA-binding protein 6	RNA.regulation of transcription.Chromatin Remodeling Factors	-	-1.1	2.6E-04	0.07	ns
Solyc01g107870.2.1	Poly(A) RNA binding protein	RNA.processing	-	-1.1	1.1E-06	-1.58	0.0E+00
Solyc09g009030.2.1	Histone deacetylase 2a-like	RNA.regulation of transcription.HDA	-	-1.3	8.8E-06	0.09	ns
Solyc04g074040.2.1	RNA-binding protein	RNA.RNA binding	-	-1.4	9.0E-04	-0.37	ns

2.4. Discussion

2.4.1. CK Effect on Phenotype under Drought Stress

The response to drought stress is a complex phenomenon controlled by crosstalk mainly between the hormones ABA and CKs, with minor contributions from other hormones for adjustment of plant metabolism. In recent years, CKs were shown to both positively and negatively regulate the abiotic stress response (Rivero et al., 2007; Merewitz et al., 2011; Werner et al., 2010; Wang et al., 2016). It was shown that constitutive expression of *IPT* caused a reduction in stature, loss of apical dominance, vascular development abnormalities and inhibition of root growth, all of which could be related to excessive CK concentration (Klee et al*.,* 1987; Hobbie et al*.,* 1994; Gan and Amasino, 1997). However, when CK levels were strictly regulated under the control of stress or senescence inducible promoters (SARK and SAG12), CK overexpression was shown to improve abiotic stress tolerance in many cases (Rivero et al., 2007; Merewitz et al., 2016). In our study, we developed transgenic tomato plants overexpressing the *IPT* gene under control of the senescence induced SARK promoter. When compared to nontransgenic lines, the transgenic plants had reductions in plant height and total biomass that correlated with *IPT* gene expression levels, which should be related to high

CK levels and could be a version of the defect that was previously shown in constitutively *IPT* overexpressing plants (Klee et al., 1987; Hobbie et al., 1994; Gan and Amasino, 1997). Under drought stress conditions, the T19 *SARK::IPT* line performed better compared to the nontransgenic line, with less severe dehydration and higher water use efficiency and with almost no leaf chlorosis. Thus, these results agree with previous research (Rivero et al., 2007; Rivero et al., 2009; Peleg et al., 2011). In a detached leaf senescence assay, the *SARK::IPT* line preserved chlorophyll content with only a slight reduction, whereas the nontransgenic line exhibit a high level of chlorophyll degradation, an indicator of leaf senescence. In previous research, CKs were shown to delay leaf senescence, reduce chlorophyll degradation and protect photosynthetic machinery, findings which are consistent with our work (Rivero et al., 2009; Cortleven et al., 2015).

2.4.2. CK Effect on Selected Metabolite Content under Drought Stress

2.4.2.1. Organic Acids

We also measured the contents of selected metabolites. We observed increased levels of the organic acids malate, citrate and pyruvate under drought stress in both nontransgenic and *SARK::IPT* lines. Malate is an organic acid which is an intermediate of the TCA (tricarboxylic acid) cycle and has an important role in energy metabolism. We determined that malate was elevated in the *SARK::IPT* line compared to the nontransgenic line both in control and drought conditions. Malate serves as a CO_2 store during carbon assimilation and also helps balance NADPH/ATP values (Scheibe, 2004). Malate was shown to increase under abiotic stress conditions in different plant species including tomato (Crecelius et al., 2003; Semels et al., 2007). We also observed an increase in pyruvate and citrate values under drought stress compared to control conditions. Citrate is also an intermediate of the TCA cycle and pyruvate is the end product of glycolysis, and their levels were elevated under drought stress conditions in tomato and other organisms (Semels et al., 2007; Merewitz et al., 2011). We also observed higher lactic acid levels in the nontransgenic line compared to the *SARK::IPT*

line under both control and drought stress conditions. Under drought stress, lactic acid increased in the *SARK::IPT* line but no significant change was observed in the nontransgenic line. Lactic acid is a product of anaerobic respiration, which is induced under water logging conditions and its accumulation is known to be potentially toxic to cellular metabolism (Felle, 2005). Higher lactic acid content can be an indicator of decreased oxidative phosphorylationas a result of the reduced leaf transpiration that occurs with drought stress.

2.4.2.2. Fatty Acids

Membrane lipid composition is of great importance for plant tolerance to environmental stress. It is known that drought and salt stress tolerance depends on levels of membrane unsaturated fatty acids and the ability to maintain these levels (Zhang et al., 2005). In previous studies, overexpression of fatty acid desaturases conferred drought tolerance in *Arabidopsis* (Zhang et al., 2012), whereas silencing of these genes resulted in abiotic stress susceptibility in tobacco and tomato (Im et al., 2002, Wang et al., 2014). In our study we observed a slight increase of palmitoleic (C16:1) and linoleic (C18:2) acid levels in the*SARK::IPT* line but a decrease in palmitoleic acid and an increase in linoleic acid levels in the nontransgenic line, which could be related to the tolerance of *SARK::IPT* to drought stress. We also observed a slight decrease in stearic acid (C18) levels in both *SARK::IPT* and nontransgenic control tomato plants under drought stress.

2.4.2.3. Amino Acids

Amino acid levels were measured and it was found that ser, trp, arg, phe, gln, glu, asn, asp, leu, lys, thr, val and pro increased under drought stress whereas ala levels were decreased in both lines (Figure 2.5). In previous work, ile, val, leu, arg, lys, pro, his, ser and gly levels were found to be significantly increased in tomato leaves under

drought stress (Joshi et al., 2010). Proline was the first amino acid identified to be associated with drought stress tolerance and to accumulate under drought stress (Singh et al., 1972). Proline accumulation is known to exert its beneficial effects by osmotic adjustment, ROS scavenging and, membranes and cellular structurestabilization (Szabados and Savoure, 2010). But in many other studies, other free amino acids were also observed to accumulate under drought stress conditions (Rai, 2002). Also more drought-tolerant plants generally accumulated relatively higher amounts of free amino acids than drought-sensitive plants (Rai, 2002). Elevated amino acids levels could contribute to drought stress tolerance by contributing to osmatic balance in both transgenic and nontransgenic line. The elevation in amino acid levels is not just caused by de novo synthesis but also caused by protein degradation. In the transgenic line we observed lower levels of amino acids compared to nontransgenic under both control and drought stress conditions. In our study three amino acid metabolism related genes were differentially abundant in nontransgenic line under drought stress and two of them were upregulated and the other one was downregulated. In the transgenic line seven amino acid metabolism related genes were differentially abundant in nontransgenic line under drought stress and two of them were upregulated and the other five of them were downregulated. The observed increase in the amino acid levels under drought stress condition was not seem to be caused by de novo amino acid biosynthesis because the levels of amino acid metabolic enzymes were decreased in both lines. So the increased amino acid l levels could be protein degradation. Despite the increase under drought stress transgenic line was observed to have lower amino acid levels compared to nontransgenic line, which could be related to the a milder increase in protein degradation in transgenic line.

2.4.3. CK Effect on Leaf Total Proteome under Drought Stress

We identified 190 proteins that showed changes in abundance due to drought stress treatment in *SARK::IPT* or nontransgenic control tomato plants (Appendix Table A.3). Of these, 71 proteins were upregulated at least 1.4 fold in the *SARK::IPT* line under drought stress conditions. A portion (23, 32%) of these upregulated genes were

also upregulated under drought stress conditions in nontransgenic control tomato plants (Figure 2.6). CKs are known to regulate gene expression in concentration, tissue and developmental stage dependent manners (Shi et al., 2013; Žd'árská et al., 2013). In a previous study, the response to exogenously applied CKs was examined at two different time points to observe early and late responses in leaf and root tissue of *Arabidopsis* (Žd'árská et al., 2013). Only a few proteins were regulatedsimilarly in the tested tissues or at the tested time points. This limited overlap could be related to the dynamic regulatory effects of CKs which could also explain the low number of differentially regulated proteins in our study that coincide with previous studies.

According to GO term enrichment analysis, the differentially regulated proteins under drought stress conditions in the *SARK::IPT* and nontransgenic lines had diverse functions including response to abiotic stimulus, sulphur compound metabolic process (mainly thioredoxin protein), oxidative stress response, chlorophyll biosynthesis, photosynthesis (mainly light harvesting and protein-chromophore linkage related proteins), isopentenyl diphosphate biosynthetic process, protein folding and primary metabolism. Gene clusters related to hormonal stimulus and oxidative stress response were the most enriched in transcriptomic profiling of the response to exogenously applied CK in *Arabidopsis* (Zwack and Rahotte, 2015). In tomato, both induced and suppressed oxidative stress response genes were identified as enriched gene clusters (Shi et al., 2013; Zwack and Rahotte, 2015). Similarly, we identified a large group of oxidative stress responsive proteins, which were grouped into the response to stimulus and especially the abiotic stimulus clusters in GO term enrichment analysis. Another important group of differentially expressed groups were photosynthesis related and chlorophyll biosynthesis related proteins.

2.4.3.1. Highly Induced Proteins under Drought Stress by CKs

In our study, lipid-transfer protein, endoribonuclease L-PSP family protein, ASR4, thylakoid lumenal 19 kDa protein, thioredoxin and REF-like stress related protein 1 were the most highly induced proteins in *SARK::IPT* lines under drought stress conditions with a fold change between 22.8 and 4.8 (Table 2.1). Plant non-

specific lipid transfer proteins (nsLTPs) have mainly lipid binding and transfer activity and are known to have various biological functions including adaptation to stress conditions (Finkinaet al., 2016). LTPs are related to plant tolerance against drought, cold and salt stress (Gangadhar et al., 2016; Jülke et al., 2015). LTPs were upregulated under heat stress conditions in potato (Gangadhar et al., 2014) and overexpression conferred heat, water-deficit and salt stresses tolerance in the same crop (Gangadhar et al., 2016). The endoribonuclease L-PSP family protein is a RidA protein which preempts reactive enamine/imine intermediates produced by Thr dehydratase (IlvA) to harmless 2-oxoacids. Enamine/imineintermediates attacs the cofactor of the Ile biosynthesis enzyme IlvE, a branched-chain aminotransferase (BCAT), by forming an adduct inactivating the enzyme.Thus RidA ensures, in an indirect manner, that isoleucine biosynthesis can proceed (Lambrecht et al., 2013). Disruption of an *Arabidopsis* homolog of the RidA protein resulted in a serine-sensitive, isoleucine-deficient phenotype in plants and reduction in root growth (Niehaus et al., 2014). ASR4 is a member of the ABA-stress-ripening (ASR) protein family which is induced by diverse physiological conditions such as fruit ripening, senescence and in response to environmental stress (González and Norerto, 2014). Overexpression of the ASR genes in different organisms conferred tolerance to several environmental stress conditions in different plant species (Li et al., 2017). Thylakoid lumenal 19 kDa protein is a grana core localized protein. Loss of function mutant plants were identified to have reduced non-photochemical quenching, affecting organization of light-harvesting complex II and enhanced grana stacking (Yokoyama et al., 2016). Thioredoxins are redox proteins known to change the redox state of proteins and have roles in protection of plants from damage caused by oxidative stress (Pulido et al., 2009; Traverso et al., 2007). REF-like stress related protein 1 is a homolog of HbSRPP proteins which have a role in rubber biosynthesis in *Hevea brasiliensis* (Berthelot et al., 2014). Homologs of SRPP proteins are also found in non-rubber producing plants areinduced by various stress conditions and involved in stress response mechanisms (Chi et al., 2016; Papdi et al., 2008). Over-expression of REF-like stress related protein 1 homologs (CaSRP1, IbMuSI and AtSRPPs) in *Arabidopsis* and tobacco resulted in enhanced drought stress tolerance (Seo et al., 2010; Kim et al., 2016). All of these highly induced proteins are related to stress tolerance, therefore; their overexpression could be related to the drought tolerance of the *SARK::IPT* line.

2.4.3.2. Antioxidant Response Related Proteins

Protection of cellular components from ROS accumulation is of great importance for plants under stress conditions because the balance between generation and removal of ROS is disturbed (Karuppanapandian et al., 2011). The antioxidant system is known to be activated as a defence mechanism against abiotic and biotic stress conditions in plants (Ahmad et al., 2010). In our study, 21 proteins which are known to be members of the antioxidant system were regulated under drought stress conditions. Specifically, 18 of these 21 differentially expressed proteins were upregulated in the *SARK::IPT* line under drought stress conditions. Six of these proteins (Solyc12g013810.1, Solyc07g063190.2, Solyc10g006970.2, Solyc04g080850.2, Solyc04g081970.2, Solyc10g078920.1) are members of the thioredoxin family. Thiol groups of cysteine residues are known to be highly sensitive to oxidation by ROS, thus their protection from oxidation is of great importance for maintenance of protein functionality under stress conditions (Maillouxet al., 2014). Thioredoxins help protect proteins from oxidative stress, act as signalling molecules by changing the redox state of proteins and some can act as co-chaperones (Balmer et al., 2004; Spoel and Loake, 2011; Prasadet al.,2010). Thioredoxins were identified to have role in oxidative stress defence and abiotic stress tolerance, which induces oxidative stress during exposure (Santos and Rey, 2006).

Glutathione is another important antioxidant system. Glutathione is used to reduce H_2O_2 metabolites via peroxidases including ascorbate peroxidase (APOX), peroxiredoxin (PRX), glutathione peroxidases (GPX) and glutathione-S-transferases (GSTs) (Kapoor et al., 2015). Another important antioxidant enzyme is glutathione reductase, which reduces oxidized GSH back to its reduced form. In our dataset, two PRX (Solyc10g082030.1 and Solyc01g007740.2), three GSTs (Solyc11g011250.1, Solyc06g009020.1 and Solyc12g094430.1), and two GPX (Solyc08g006720.2 and Solyc12g056230.1) proteins were upregulated in the *SARK::IPT* line under drought stress. In previous studies transgenic plants overexpressing the *IPT* gene were identified to have higher antioxidant capacity (Dertinger et al., 2003) and to resist a virus-induced hypersensitive response by efficient ROS scavenging (Pogany et al., 2004). In a previous transcriptomic study, CKs were identified to regulate genes related to response

to oxidative stress with a high percentage of proteins with redox-associated enzyme activities (Brenner et al., 2012). We observed induction of many oxidative stress responsive enzymes in transgenic line compared to nontransgenic, which is an indicator for a better oxdative stress defence systema and as a result lower levels lipid peroxidation as is observed in our study.

2.4.3.3. Chloroplastic Proteins

Chloroplastic proteins are the major group of proteins regulated by CKs (Černý et al., 2013). Accordingly, in our dataset, the largest group of proteins (62%) regulated by drought stress and CKs were chloroplastic proteins. Altered CK levels regulated many different aspects of chloroplasts, including chlorophyll synthesis, chloroplast ultrastructure organization, photosynthesis fine-tuning, chloroplast division and gene expression (Corleven and Schmulling, 2015). Also it was found that loss of CK signalling caused increased photooxidative damage to the photosynthetic machinery, an important indication of the protective effect of CKs on the photosynthetic apparatus (Cortleven et al., 2014). Drought is known to reduce photosynthetic activity due to the decreased CO_2 conductance caused by stomatal closure, limitations in mesophyll tissue, alterations in photosynthetic metabolism and damageto photosynthetic proteins by increased oxidative stress (Chaves et al., 2009). In our study, we observed many changes in expression levels in chlorophyll biosynthetic enzymes, components of photosynthetic complexes and antioxidant proteins. Six CAB proteins (Solyc03g005780.1, Solyc02g071000.1, Solyc12g011450.1, Solyc12g011280.1, Solyc01g105030.2, Solyc06g063370.2) were upregulated in the *SARK::IPT* line under drought stress condition, whereas most of these proteins were downregulated in the nontransgenic line. Chlorophyll a/b-binding proteins (CAB) bind and coordinate the function of antenna pigments in the light-harvesting complex (LHC) in bothphotosystems (PS), I and II, (Jansson, 1994). CAB proteins directly bind to chlorophyll and chlorophyll degradation takes place with loosening of chlorophyll CAB protein complexes followed by degradation of both chlorophyll and CAB proteins (Park et al., 2007). CAB protein expression levels are downregulated during leaf senescence

(Grbić and Bleecker, 1995) and are regulated by ABA (Xu et al., 2012). Upregulation of CAB proteins could be related to maintenance of the antenna complex in LHC, thus protecting functional chlorophyll from degradation and maintaining the photosynthetic complex in the *SARK::IPT* line under drought stress. Other proteins which are part of the photosynthetic machinery were also upregulated in the *SARK::IPT* line under drought stress, including photosystem I reaction center subunit VI-1, photosystem I reaction centre subunit XI, photosystem I reaction centre subunit N, PsbP domain-containing protein 6, thylakoid lumenal 19 kDa protein, oxygen-evolving enhancer protein 3 and proton gradient regulation 5. Proteincomponents of the photosynthetic complex were also upregulated in *SARK::IPT* tobacco under drought stress conditions (Rivero et al., 2010). Components of photosystem I (PSI) are of great importance for both linear electron transport for production of ATP and NADPH and for cyclic electron transport (CET) for production of just ATP. CET is known to be activated during drought and to be a crucial mechanism for preventing PSI and PSII damage caused by environmental stress (Huang et al., 2012). Proton gradient regulation 5 is required for activation of CET (Long et al., 2008). In our study, components of PSI and proton gradient regulation 5 were upregulated in *SARK::IPT* transgenic plants, which could activate CET for improved tolerance to drought. Both PBSP and PBSQ proteins which are Photosystem II (PSII) oxygen evolving complex proteins were also upregulated in *SARK::IPT* transgenic plants and are known to stabilize the PSII-LHC complex (Allahverdiyeva et al., 2013). RUB and its regulator RuBisCO activase also have great importance for CO_2 assimilation. The small subunit of RuBisCO is known to regulate the carboxylase/oxygenase activity of the enzyme. Knockdown mutants of the subunit have suppressed photorespiration (Dhingra et al., 2004). In our experiments we observed an increase in RuBisCO small subunit levels in *SARK::IPT* plants, whereas a decrease was observed in nontransgenic plants. RuBisCO activase is the key enzyme which has a role in re-activation of post-translationally modified Rubisco. Reduction in RuBisCO activase levels was identified to be a key factor for repression of RuBisCO activity (Lawlor and Tezara, 2009). We observed downregulation of RuBisCO activase in both nontransgenic and transgenic lines under drought stress conditions, however; the reduction was lower in *SARK::IPT* line. A milder reduction in RuBisCO activase levels could be related to a less impairment of RuBisCO activity compared to nontransgenic line and milder reduction in production in sugars in transgenic line.

In *SARK::IPT* plants we observed higher chlorophyll a and b levels compared to nontransgenic plants under control conditions and a slight reduction under drought stress condition with no significant difference between *SARK::IPT* and nontransgenic plants. We observed a reduction in the expression of six chlorophyll biosynthesis related enzymes (Solyc03g118240.2, Solyc10g077040.1, Solyc10g008740.2, Solyc07g054210.2, Solyc03g115980.1, Solyc04g009200.2) under drought stress in both the *SARK::IPT* and nontransgenic line (Appendix Table A.3). In the *SARK::IPT* line, chlorophyll synthase (CHLG) was upregulated (1.8 fold) under drought stress. CHLG catalyses the last step of the chlorophyll biosynthetic pathway by esterification of chlorophyllide a and b with phytyl or geranyl-geranyl pyrophosphate in chloroplasts (Eckhardt et al., 2004). It is known that intermediates of chlorophyll synthesis especially chlorophyllide a and b produce singlet oxygen which causes oxidative stress damage in chloroplasts (Hörtensteine, 2006). Chlorophyll synthase re-esterifies the chlorophyllide produced during chlorophyll turnover, thus it acts as a salvage pathway. It prevents accumulation of phototoxic chlorophyll intermediate and reproduces active chlorophyll b from de-assembled chlorophyll (Lin et al., 2014). Under drought stress conditions reduction of the accumulation of phototoxic chlorophyll intermediates and reproduction of active chlorophyll produced from chlorophyll turnover could have great importance for protection of the photosynthetic machinery and maintenance of chlorophyll levels. Thus, CHLG could replenish active chlorophyll pools via turn-over, independent from de novo synthesis. Also increased CAB overexpression could reduce chlorophyll degradation in *SARK::IPT* plants, which could contribute to maintenance of the active chlorophyll pool. Moreover *Arabidopsis* homologs of 14 oxidative stress responsive genes were identified to be located in chloroplasts which could also help protect chloroplatic proteins, including chloroplast biosynthetic enzymes from oxidative damage, thus the turn-over time could be extended. Increased levels of CHLG, CABs and antioxidative proteins could compensate for the reduced expression of other chlorophyll biosynthetic enzymes.

2.4.3.4. Hormone Metabolism Related Proteins

Hormones are the major regulators of the plant response to drought stress. In our dataset we identified five differentially regulated proteins related to hormone metabolism. Zeaxantin epoxidase (ZEP) is the enzyme catalysing the first step of ABA synthesis (Marin et al., 1996); however, it is not the limiting enzyme in biosynthesis of this hormone (Xiong and Zhu, 2003). ZEP products are also involved in the light-harvesting complex in the xanthophyll lcycle. In tomato overexpression of ZEP caused decreased maximal photochemical efficiency of PSII and reduced recovery during stress conditions, which had a negative effect on stress tolerance (Wang et al., 2008). In our study, ZEP was down regulated in *SARK::IPT* transgenic plants but not significantly changed in nontransgenic plants under drought stress, which could be an adaptation for protection of the light harvesting complex under stress. Allene oxide synthase (AOS) is an enzyme in the jasmonic acid (JA) biosynthetic pathway and was downregulated in *SARK::IPT* transgenic lines under drought stress in our study. 2-oxo-phytodienoic acid (12-OPDA) is a precursor of JA and is produced by AOS (Liavonchanka and Feussner, 2006). In previous studies, 12-OPDA was shown to be involved in stomatal closure together with ABA (Savchenko et al., 2014). 1-aminocyclopropane-1-carboxylate oxidase (ACO) is an ethylene biosynthetic enzyme and was upregulated in both *SARK::IPT* transgenic (1.9 fold) and nontransgenic (2.8 fold) lines under drought stress conditions. ACO and ethylene levels are induced during senescence, fruit ripening in tomato (Blume and Grierson, 1997) and water deprivation conditions (Voisin et al., 2006). Gibberellin 2-beta-dioxygenase is an enzyme involved in gibberellic acid (GA) deactivation (Sponsel and Hedden, 2010) and was upregulated in the nontransgenic line (1.7 fold) and downregulated (1.45 fold) in *SARK::IPT* transgenic plants. GA content was reduced by abiotic stress and was accompanied by reduced growth and photosynthesis rate under such conditions (Yoon et al., 2009; Hamayun et al., 2010). Downregulation of this GA inactivating enzyme could contribute to maintenance of GA levels under drought stress in the *SARK::IPT* transgenic line. Auxin-repressed protein (ARP) is a negative regulator of auxin signalling and causes inhibition of vegetative growth (Lee et al., 2013). *Arabidopsis* ARP proteins are upregulated by abiotic stress conditions (Rae et al., 2013). In our study the ARP gene was upregulated both in

nontransgenic and *SARK::IPT* transgenic lines with a higher induction in *SARK::IPT*, which could be associated with growth reduction by drought stress. DWARF1 encodes an enzyme with a role in the brassinosteroid biosynthetic pathway and was downregulated in *SARK::IPT* transgenic lines under drought stress, which could also be related to plant growth reduction under drought stress.

2.4.3.5. Amino Acid Metabolism Related Proteins

In previous work, ile, val, leu, arg, ala, lys, pro, his, ser and gly levels were significantly increased in tomato leaves under drought stress conditions (Joshi et al., 2010). In our experiments, ser, trp, arg, phe, gln, glu, asn, asp, leu, lys, thr, val and pro increased whereas ala levels decreased under drought stress in both lines. Because amino acid levels were regulated under drought stress condition, it was not surprising that 12 proteins related to amino acid metabolism were differentially regulated. Of these, four proteins were related to arg metabolism. Arg is one of the major intermediates for storage and transport of nitrogen. It also serves as a precursor for amino acid and polyamine biosynthesis (Braucet al., 2012). Polyamines are known to have osmoprotectant roles in osmotic stress conditions. Differential regulation of the arg metabolic enzymes NOAD, VEN3, OTC and ARG1 could have an important role in regulation of arginine and polyamine levels under drought stress. Also a pro catabolic enzyme, P5CDH, was overexpressed in both *SARK::IPT* and nontransgenic lines. Over-accumulation of pro in *Arabidopsis* induced heat stress susceptibility because of ROS accumulation during proline/P5C (pro precursor) cycling (Lv et al., 2011). Overexpression of P5CDH could be an adaptive mechanism for tolerating drought stress by breaking down overaccumulated pro.

2.4.3.6. Heat Shock Proteins

Heat shock proteins (HSPs) have a regulatory role for protein folding, targeting to specific locations and targeting the proteins to degradation (Feder and Hofman, 1999). Diverse stress conditions induce the synthesis of HSPs (Swindell et al., 2007). In our dataset, six HSPs and chaperonin protein were differentially regulated under drought stress in the *SARK::IPT* or nontransgenic line. A 10 kDa heat shock protein which is known to be involved in unfolded protein response was upregulated both in the *SARK::IPT* and nontransgenic lines. Heat shock cognate protein 80 (HSC80) is a negative regulator of drought and salt stress and its upregulation reduced drought and salt tolerance in *Arabidopsis* (Song et al., 2009). HSC80 was downregulated in the *SARK::IPT* line and slightly upregulated in the nontransgenic line under drought stress conditions, which could contribute to the drought stress tolerance of the *SARK::IPT* line. Chloroplast chaperonin 10 (Cpn10) is a chaperonin with a role in the unfolded protein response and was identified to be involved in RuBisCO folding (Hauser et al., 2015). This protein was slightly upregulated in the *SARK::IPT* line and no significant change was observed in the nontransgenic line under drought stress conditions. LEA (late embryogenesis abundant) proteins are involved in diverse physiological events and are considered predominantly to participate in protection of cellular components from dehydration by different proposed mechanisms including, formation of a solvation shell around the macromolecules, protecting them from interaction with ROS and acting as chaperonins (Shih et al., 2008). Osmotin-like protein was upregulated in both *SARK::IPT* and nontransgenic lines under drought stress, with a higher induction in the *SARK::IPT* line. This protein was identified to be a LEA protein involved in desiccation tolerance (Sharma et al., 2013). LEA-like protein was identified to be upregulated in the nontransgenic line under drought stress but no significant change was observed in the *SARK::IPT* line.

2.4.3.7. Protein Catabolism Related Proteins

Increased protease gene expression is observed both in senescence and under various environmental stresses. Proteases are involved in aging and stress related events such as degradation of damaged or unnecessary proteins, nutrient remobilization and remodeling of cell protein components (Martinez et al., 2007). However, proteases are suggested to act differenetly under drought stress conditions compared to senescence in terms of expression patterns (Pesquet, 2012). In our dataset, 12 proteolytic proteins were differentially regulated in the *SARK::IPT* or nontransgenic line under drought stress conditions.

CYP3, CYP1 and APs are involved in the senescence process (Gepstein et al., 2003; Simões and Faro, 2004). CYP3 was upregulated under drought stress in both the *SARK::IPT* and nontransgenic lines, which could be an indicator of abiotic stress associated leaf senescence (Munné-Bosch and Alegre, 2004). In contrast, Cathepsin B-like cysteine proteinase was upregulated under drought stress only in the nontransgenic line. Similarly AP was upregulated in the nontransgenic line but downregulated in *SARK::IPT* under drought stress. The peptidase M50 family homolog of *Arabidopsis* was identified to be involved in the heat shock response (Nishizawa et al., 2006), ethylene response and chloroplast development (Chen et al., 2005). A peptidase M50 family protein was upregulated under drought stress conditions in the nontransgenic line but no significant change was observed in the *SARK::IPT* line. Three ATP-dependent Clp protease subunits were differentially regulated in the *SARK::IPT* and nontransgenic lines. These subunits are known to be involved in regulation of plastid function (Olinares et al., 2011). Kunitz trypsin inhibitor 4 (KTI4) was upregulated under drought and flooding in *Solanum dulcamara* (Nguyen et al., 2016). In our dataset KTI4 was upregulated in *SARK::IPT* but highly downregulated in the nontransgenic line under drought stress, which could reduce the activity of the active proteases.

2.4.4. CK Effect on Leaf Nuclear Enriched Proteome under Drought Stress

We identified 81 proteinswith abundance changes due to drought stress treatment in the *SARK::IPT* and nontransgenic control tomato plants in nuclear enriched protein extracts. Of these, 43 (63.2%) proteins were upregulated in *SARK::IPT* lines under drought stress conditions, and were induced at least 1.4 fold after drought stress treatment. Three of these upregulated genes were also upregulated under drought stress conditions in nontransgenic control tomato plants. These differentially regulated genes have diverse functions including RNA processing and binding, transcription regulation, protein degradation and signalling.

2.4.4.1. Highly Induced Nuclear Enriched Proteins under Drought Stress by CKs

The most highly induced four proteins had fold changes from 6.2 to 2.1 in *SARK::IPT* plants under drought stressand were: dehydrin, H1 histone-like protein, senescence-associated protein DIN1, transcriptional activator protein Pur-alpha (Table.2.2). Dehydrin (SILEA10) is a late embryogenesis abundant protein (LEA), which is induced under stress conditions and helps cellular proteins retain their functions. LEA proteins can reside in different compartments within the cell including nuclei (Hincha and Thalhammer, 2012). SILEA10 was previously identified to be upregulated under water and salinity stress conditions (Coa and Li, 2015). H1 histone-like protein was upregulated 3.1 fold in *SARK::IPT* plants under drought stress conditions. H1 histone-like protein regulates the accessibility of chromatin DNA to trans-acting factors (Izzo et al., 2008). The *Arabidopsis* homolog of tomato H1 histone-like protein was upregulated under drought stress conditions (Ascenzi et al., 1997) and also in response to ABA and ABA-regulated transcription factors (Zang et al., 2008; Huang et al., 2008). Senescence-associated protein DIN1 is a proteosome subunit beta type protein (PBC2) and was upregulated 2.5 fold in *SARK::IPT* plants under drought

stress.The *Arabidopsis* homolog of tomato PBC2 protein was upregulated immediately after treatment with genotoxin, and could have a role in damage repair after genotoxin exposure (Cheng et al., 2003). Transcriptional activator protein Pur-alpha is known to bind to single stranded DNA and has a role in DNA replication and transcription and unknown physiological function in plants (Knapp et al., 2006). Transcriptional activator protein Pur-alpha was upregulated 2.3 fold in *SARK::IPT* plants under drought stress conditions. Some of these strongly upregulated proteins were already known to be associated with abiotic stress tolerance and all could have important roles in drought tolerance of *SARK::IPT* plants.

2.4.4.2. Transcription Factors

In our nuclear enriched proteome analysis, 16 transcription factors were differentially regulated under drought stress in *SARK::IPT* or nontransgenic lines (Appendix Table A.4). Transcription factors directly control gene expression in response to signals that are transmitted into the nuclei. Environmental and hormonal signals induce signal transduction pathways and finally regulate the transcription factors for changing gene expression to generate an adaptive response to the existing situation (Seki et al., 2007). Thus understanding the regulation of transcription factors could contribute to understand the CK and drought stress responses. There is no information about the biological roles in tomato or *Arabidopsis* for most of the identified transcription factors.However, some could have roles in the drought or CK response based on their roles in *Arabidopsis*. These transcription factors are: Solyc01g009080.2.1, Solyc10g081030.1.1, Solyc03g117780.2.1, Solyc01g007070.2.1, Solyc03g123530.2.1, Solyc08g080580.2.1, Solyc01g107330.2.1, Solyc02g068100.2.1. FHA domain containing protein which is a transcription factor and *Arabidopsis* homolog of the gene encoding SMAD/FHA was identified to be regulated under abiotic stress conditions (Rassmussen et al., 2013). Nascent polypeptide-associated complex alpha subunit-like protein is a homolog of *Arabidopsis*, is related to floral organ morphogenesis (Xie et al., 2015) and is also a salinity stress responsive protein (Jiang et al., 2007). The ubiquitin receptor RAD23 family protein acts as an ubiquitin receptor

and a shuffling factor targeting proteins to proteosome degradation (Elsasser et al., 2004). RAD23 was first identified to function as a DNA repair factor with a role in nucleotide excision repair in UV light damaged DNA (Guzder et al., 1998; Sturm and Lienhard 1998). In addition, this protein has a role in ABA signalling (Zhang et al., 2005) and was upregulated under abiotic stress (Na et al., 2017). The BEL1-like homeodomain protein 1 family transcription factor was downregulated in *SARK::IPT* (1.7 fold) and upregulated in nontransgenic plants (1.7 fold) under drought stress. BLH 1 is an ABA-induced gene (Guo et al., 2009). BLH 1 was upregulated under drought stress conditions in poplar and mandarin (Yoon et al., 2014; Gimeno et al., 2009). CCAAT-box-binding transcription factor-like protein was downregulated in *SARK::IPT* plants (1.8 fold) under drought stress. Loss of function mutants of the *Arabidopsis* homolog of this protein (EDA25) were aluminium sensitive and had lower level of polyamine biosynthesis (Nezames et al., 2013). This gene was also differentially regulated under drought stress (Ding et al., 2013). A Myb family transcription factor was upregulated in both lines under drought stress. *Arabidopsis* has two homologs of Myb family transcription factor; *MYB3R1* and *MYB3R4*. *MYB3R1* and *MYB3R4* induce cytokinesis via transcriptional regulation (Haga et al., 2007). MYB3R1 activates a variety of genes that are expressed specifically during the G2 and M phases of the cell cycle and repress cell proliferation (Haga et al., 2011). The SWIB_MDM2 domain protein is a subunit of the SWI/SNF protein complex which has a role in chromatin remodelling (Bennett-Lovsey et al., 2002). This protein was strongly downregulated in nontransgenic plants, whereas its expression did not change significantly in the *SARK::IPT* line. The *Arabidopsis* homolog of SWIB_MDM2 domain protein was responsive to ethylene and downregulated with ethylene treatment (De Paepe et al., 2004). The SWI/SNF complex component protein 12 is another part of the SWI/SNF protein complex and was upregulated in the *SARK::IPT* line and downregulated in the nontransgenic line. *Arabidopsis* homolog BAF60 negatively regulates expression of *IPT* genes in root meristem (Jegu et al., 2015).

2.4.4.3. Other Protein Groups

Gene expression is controlled at transcriptional and posttranscriptional levels. RNA binding proteins are the major agents contolling transcriptional and posttranscriptional RNA regulation and theyare known to be involved in the stress response (Lorković, 2009). In our nuclear enriched proteome profiling, the most enriched group of proteins were other nucleic acid binding proteins with 18 proteins having roles in RNA binding, processing, transcription regulation and DNA synthesis. The third most enriched group was proteins related to proteolysis containing proteosome related proteins, E3 ligases and other proteases. The proteosome protein degradation pathway plays an important role in the plant stress response by regulating protein half time, which could enable accomplishment of the suitable process during stress response (Kupera et al., 2009). We also identified three proteins with chaperonin activity and two proteins with LEA activity, which are known to be related to stress response.With the exception of Hsp90 , all of the other proteins: HSP17.8-CI , HSP70-1, dehydrin and LEA, were upregulated in the *SARK::IPT* line under drought stress and could be related to the drought stress tolerant phenotype of the *SARK::IPT* line. In our nuclear enriched proteome dataset, we also observed differential expression of proteins related to protein import, structural proteins and signal transduction molecules.

2.5. Conclusion

We developed transgenic tomato plants overexpressing the *IPT* gene under control of the *SARK* promoter and we evaluated the plant growth and yield parameter as detailed in Chapter I. We observed some defects in the *SARK::IPT* homozygous lines after flowering. However, normal plant growth properties were observed for both T6 and T19*SARK::IPT* homozygous and hemizygous plants before flowering. It was previously reported that a controlled increase in CK levels provides improved tolerance to abiotic stresses in transgenic plants overexpressing the *IPT* gene. Therefore, we tested ourT19 *SARK::IPT* transgenic line and nontransgenic line to evaluate the drought

stress response before flowering. Drought stress was applied by withholding water for two week. The *SARK::IPT* line performed better under drought stress compared to the nontransgenic line interms of phenotypic and biochemical traits. The *SARK::IPT* line had less reduction in fresh weight and relative water use efficiency under drought stress conditions compared to nontransgenic. In addition, the accumulation of the lipid peroxidation indicator MDA was lower in the *SARK::IPT* line compared to the nontransgenicline under both control and drought stress. Moreover, chlorophyll degradation and senescence were reduced in the *SARK::IPT* line. Because improved drought tolerance was observed in *SARK::IPT* line in terms of water use efficiency, antioxidant system and delayed senescence, we conducted a proteomics analysis for understanding the molecular mechanisms of these phenomena. We also measured the relative levels of 15 proteogenic amino acids, some organic acids and fatty acids, to evaluate their roles in the drought response of the tested lines. Level of most of amino acids (proline, arginine, asparagines, glutamine, glutamic acid, leucine, lysine, phenylalanine, tryptophan, valine and aspartic acid, serine and threonine) increased in both *SARK::IPT*and nontransgenic lines under drought stress.It is known that free aminoacid levels increase under abiotic stresses both as a result of de novo synthesis and from protein degradation. In our study increased levels of malic, citric, pyruvic and lactic acid were seen in both *SARK::IPT*and nontransgenic lines under drought stress. Previously, increased levels of malic, citric and pyruvic acid levels were reported under stress and hypothesized to be related to adjustment of cellular pH, cellular ionic balance and synthesis of fatty acids and other metabolites. In our study, increased levels of palmitoleic (C16:1), linoleic (C18:2) and heptadecanoic (C17) acid were measured in the*SARK::IPT* line under drought stress. Increased levels of unsaturated fatty acids such as palmitoleic (C16:1) and linoleic (C18:2) were observed as an adaptation to drought stress. From the shotgun proteomic analysis of the mature leaf total proteome we identified around 190 proteins with altered abundances in either *SARK::IPT* or nontransgenic control tomato plants. Of these 190 differentially abundant proteins,response to abiotic stimulus, sulfur compound metabolic process (mainly thioredoxin protein), oxidative stress response, chlorophyll biosynthesis, photosynthesis (mainly light harvesting and protein-chromophore linkage related proteins), isopentenyl diphosphate biosynthetic process, protein folding and primary metabolism were the most enriched GO terms. In MAPMAN categories, redox related group was the third largest protein group, with around 79% of the differentially abundant redox proteins

upregulated under drought stress. Activation of oxidative stress responsive genes was also reported in other studies investigating the impact of increased CK levels. Thioredoxins are known to regulate the redox state of proteins by regulating the oxidation state of cysteine residues and are reported to have a role in stress tolerance. In our study, six thioredoxin paralogs were upregulated under drought stress in the *SARK::IPT* line, which could have beneficial roles in drought stress tolerance. Moreover, antioxidant enzymes including two peroxiredoxin, three glutathione S-transferase and two glutathione reductase isozymes were upregulated in the *SARK::IPT* line, which could contribute to scavenging of ROS produced during drought stress. In the *SARK::IPT* line, the MAPMAN category for photosynthesis related proteins was the largest group of differentially abundant proteins in response to drought stress. Moreover, around 60% of differentially abundant photosynthetic proteins were upregulated by drought stress in transgenic plants. In contrast, all differentially abundant photosynthesis related proteins were downregulated in the nontransgenic line under drought stress, which can be a sign of stress. CKs are known to have roles in chloroplast development and in the regulation of photosynthetic activity. Moreover CKs are important in preservation of photosynthetic activity under stress conditions, which can be associated with strong regulation of chloroplastic genes by CKs as was observed in our study. In our study, six CAB (chlorophyll a/b binding) proteins having a rolein cyclin electron transport in PS I, oxygen evolving complex subunits, and RuBisCo small subunit were upregulated in the *SARK::IPT*line under drought stress, which could contribute to chlorophyll stabilization, PSII-LHC complex and prevention of oxidative damage to PSI and PSII. Protein metabolism was the second largest group of differentially abundant proteins in the transgenic *SARK::IPT* line and the most abundant group for the nontrangenic line under drought stress conditions. Protein degradation is known to be accelerated and synthesis suppressed by stress. The profile of protein synthesis and degradation related proteins in *SARK::IPT* line was in agreement with this knowledge. In our study, senescence induced CYP3, CYP3 and APs proteinases were upregulated and kunitz trypsin inhibitor, which acts as a proteinase inhibitor was upregulated in the *SARK::IPT* line under drought stress. Stress and/or ABA responsive proteins such as beta-tonoplast intrinsic protein, non-specific lipid-transfer protein, ASR4, thioredoxin, REF-like stress related protein 1 and PAP fibrillinwere among the ten most highly upregulated proteins in the *SARK::IPT* line, which could contribute to stress tolerance. Three chloroplastic proteins including thylakoid lumenal 19 kDa

protein, chlorophyll a-b binding protein 8 and oxygen-evolving enhancer protein 3were among the ten most highly upregulated proteins in the transgenic line, which could contribute to stabilization of the photosynthetic machinery under drought stress and, thereby,contribute to tolerance. Four chlorophyll biosynthetic enzymes including protochlorophyllide reductase, magnesium-protoporphyrin IX monomethyl esteroxidative cyclise and geranylgeranyl reductase were among the ten most strongly downregulated proteins in the *SARK::IPT* line. Although we observed reduced degradation rate of chlorophyll in the *SARK::IPT* line, de novo synthesis seems to be repressed under drought stress.

We also conducted shotgun proteomic analysis from the leaf nuclear enriched protein extract to investigate the regulation of gene transcription under drought stress conditions. A total of 81 proteins were differentially abundant in response to drought stress in either the *SARK::IPT* or nontransgenic line, which could potentially be localized in the nucleus. Of these 81 differentially abundant proteins, 18 transcription factors, 3 RNA processing enzymes, 11 RNA binding proteins, 6 DNA synthesis and/or chromatin structure related proteins, a DNA repair protein and a DNA binding protein had differential abundance under drought stress conditions, and could have roles in regulation of transcription or transcript stability under drought stress. Other proteins with roles in protein degradation, targeting, cytoskeleton organization, signaling and abiotic stress response were differentially abundant in either the *SARK::IPT* line or the nontransgenic line under drought stress. In previous studies, orthologs of transcription factor FHA domain containing protein, nascent polypeptide-associated complex alpha subunit-like protein, RAD23 family protein , and the BEL1-like homeodomain protein 1 family transcription factor were found to be involved in the stress responsesof different plant species but no detailed information is available for these proteins. The genes for interesting candidate proteins could be cloned and overexpressed in tomato to evaluate the effect of increased expression levels on plant growth and development under normal and drought stress conditions. Alternatively, the interesting genes can be silenced by siRNA or CRISPR-CAS9 methods to investigate the effect of reduced protein levels on normal plant growth and development or under drought stress conditions.

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APPENDIX

SUPPLEMENTARY FIGURES AND TABLES

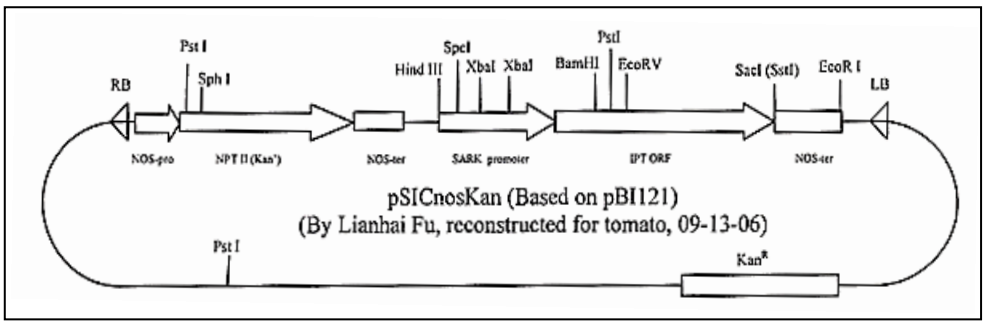

Figure A.1 pSICnosKan plasmid map.

Table A.1. Sequence information for the primers used in the study

pSARKIPT	Seqences	TM	Size (bp)
forward primer	TTCTTCCTTAGATGCTGTCACAA	61	1400
reverse primer	GAACATCTTATCCAGATGAAGACAGG		
pSarkF1/iptR1		TM	Size (bp)
forward primer	TCGTTCCTTTCAGTTCTTCC	63	600
reverse primer	CCAACTTGCACAGGAAAGAC		
IPT_105-267		TM	Size (bp)
forward primer	GGCTTCCAGTCCTTTCGCTT	63	162
reverse primer	GTCGTTCCTTTCAGTTCTTCCAC		
IPT_354-520		TM	Size (bp)
left primer	CCACAAGTTACCCGACCAAGAG	63	166
reverse primer	CAGCCGAGGTTCATTCCAAAG		
TIP41		TM	Size (bp)
forward primer	ATGGAGTTTTTGAGTCTTCTGC	60	235
reverse primer	GCTGCGTTTCTGGCTTAGG		
CAC		TM	Size (bp)
forward primer	CCTCCGTTGTGATGTAACTGG	60	173
reverse primer	ATTGGTGGAAAGTAACATCATCG		
Ubiquitin		TM	Size (bp)
forward primer	ACCAAGCCAAAGAAGATCAAGC	60	173
reverse primer	ATTGGTGGAAAGTAACATCATCG		
Ribosomal protein L2		TM	Size (bp)
forward primer	GTCATCCTTTCAGGTACAAGCA	60	156
reverse primer	CGTTACAAACAACAGCTCCTTC		

Table A. 2. List of proteins differentially regulated in transgenic and nontransgenic plants grown under normal conditions.

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc07g047850.2.1	1	Chlorophyll a-b binding protein 4, chloroplastic	PS.lightreaction.photosystem II.LHC-II	-1	5.2E-02	-0.3	ns	-0.2	ns	-0.1	ns
solyc11g039980.1.1	1	Uncharacterized protein	PS.lightreaction.ATP synthase	1.1	1.1E-03	0.4	ns	0.2	ns	0.2	ns
solyc05g008450.2.1	1	Uncharacterized protein	PS.lightreaction.other electron carrier (ox/red).ferredoxin oxireductase	0.2	ns	-0.9	ns	-1.2	ns	-0.3	ns
solyc02g084440.2.1	1	Fructose-bisphosphate aldolase	PS.calvin cycle.aldolase	-0.3	ns	-0.8	2.4E-02	-0.4	ns	0	ns
solyc02g062340.2.1	1	Fructose-bisphosphate aldolase	PS.calvin cycle.aldolase	-0.4	ns	-0.9	1.7E-02	-0.5	2.0E-02	-0.1	ns
solyc10g083570.1.1	1	Fructose-bisphosphate aldolase	PS.calvin cycle.aldolase	0.7	2.0E-03	-0.2	ns	-0.1	ns	0.1	ns
solyc09g009260.2.1	1	Fructose-bisphosphate aldolase	PS.calvin cycle.aldolase	0.9	8.8E-04	0.1	ns	0.2	ns	0.2	ns
solyc10g086720.1.1	1	Uncharacterized protein	PS.calvin cycle.FBPase	0.4	4.1E-02	-0.8	ns	-0.6	ns	-0.4	ns
solyc01g014210.1.1	1	Uncharacterized protein	major CHO metabolism.synthesis.starch.transporter	0.1	ns	0.6	1.9E-02	0.3	ns	0	ns
solyc02g091490.2.1	1	Uncharacterized protein	major CHO metabolism.degradation.sucrose.fructokinase	-0.6	ns	0.5	4.0E-02	1.3	2.1E-03	0	ns
solyc11g067160.1.1	1	Uncharacterized protein	minor CHO metabolism.others	0.9	ns	0.4	ns	-1.2	ns	0.3	ns
solyc06g053600.2.1	1	Uncharacterized protein	minor CHO metabolism.others	0.9	5.1E-02	0.5	ns	-0.4	ns	0.5	ns
solyc01g080460.2.1	1	Uncharacterized protein	gluconeogenese/ glyoxylate cycle.pyruvate dikinase	0.6	ns	-0.5	ns	-0.4	ns	-0.3	ns
solyc04g005080.2.1	1	Pyruvate dehydrogenase E1 component subunit alpha	TCA / org. transformation.TCA.pyruvate DH.E1	0.9	5.0E-02	-0.1	ns	-1.2	ns	-0.8	ns
solyc06g072580.2.1	1	Uncharacterized protein	TCA / org. transformation.TCA.pyruvate DH.E1	1.8	2.7E-04	0.9	3.7E-02	0.3	ns	0	ns
solyc12g005860.1.1	1	Aconitate hydratase	TCA / org. transformation.TCA.aconitase	0.2	ns	0.5	1.4E-02	0.4	ns	0.3	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc02g082860.2.1	1	Uncharacterized protein	TCA / org. transformation.TCA.IDH	0.1	ns	0.8	6.9E-03	0.6	ns	0.2	ns
solyc04g011350.2.1	1	Uncharacterized protein	TCA / org. transformation.TCA.2-oxoglutarate dehydrogenase	2	1.0E-02	1.2	5.1E-02	0.6	ns	0.6	ns
solyc06g083790.2.1	1	Succinyl-CoA ligase subunit beta	TCA / org. transformation.TCA.succinyl-CoA ligase	0.3	5.1E-02	0.5	1.5E-02	0.6	ns	0.1	ns
solyc01g007910.2.1	1	Succinyl-CoA ligase [ADP-forming] subunit alpha-1, mitochondrial	TCA / org. transformation.TCA.succinyl-CoA ligase	1.3	3.3E-03	0.6	1.6E-02	0.5	ns	0.4	ns
solyc12g014180.1.1	1	Malate dehydrogenase	TCA / org. transformation.TCA.malate DH	0.9	4.8E-02	-0.1	ns	0	ns	0.1	ns
solyc10g008140.2.1	1	Uncharacterized protein	mitochondrial electron transport / ATP synthesis.NADH-DH.complex I	1.4	2.9E-03	0.7	4.9E-02	0.4	ns	0.4	ns
solyc00g042130.1.1	1	Uncharacterized protein	mitochondrial electron transport / ATP synthesis.F1-ATPase	-0.4	ns	-0.8	ns	-0.5	1.4E-02	-0.2	ns
solyc01g111760.2.1	1	Uncharacterized protein	mitochondrial electron transport / ATP synthesis.F1-ATPase	1	2.3E-04	1	1.6E-04	0.9	5.8E-03	0.3	ns
solyc10g055670.1.1	1	Uncharacterized protein	mitochondrial electron transport / ATP synthesis.F1-ATPase	1.1	1.4E-04	1	2.0E-04	0.9	8.4E-03	0.4	ns
solyc10g055670.1.1	1	Uncharacterized protein	transport.p- and v-ATPases.H+-transporting two-sector ATPase.subunit B	1.1	1.4E-04	1	2.0E-04	0.9	8.4E-03	0.4	ns
solyc03g033440.1.1	1	Uncharacterized protein	mitochondrial electron transport / ATP synthesis.F1-ATPase	0.6	3.0E-02	0.5	ns	-0.1	ns	-0.1	ns
solyc11g072450.1.1	1	Uncharacterized protein	mitochondrial electron transport / ATP synthesis.F1-ATPase	1.3	5.5E-03	0.9	4.3E-02	0.5	ns	0.5	ns
solyc01g087120.2.1	1	Uncharacterized protein	mitochondrial electron transport / ATP synthesis.F1-ATPase	1.8	3.0E-03	1	9.8E-03	0.6	ns	0.4	ns
solyc01g098240.1.1	1	Uncharacterized protein	cell wall.cell wall proteins.HRGP	0	2.2E-03	-1.1	ns	-0.7	ns	-0.5	ns
solyc03g123630.2.1	1	Pectinesterase	cell wall.pectin*esterases.PME	0.8	1.8E-02	0.7	2.8E-02	0.5	ns	-0.1	ns
solyc01g006980.2.1	1	Uncharacterized protein	lipid metabolism.FA synthesis and FA elongation.Acetyl CoA Transacylase	1.9	9.7E-03	1	5.1E-02	0.7	ns	0.9	ns
solyc05g015490.2.1	1	Uncharacterized protein	lipid metabolism.lipid transfer proteins etc	0.5	ns	1.7	9.4E-05	0.6	ns	0.2	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc10g075150.1.1	1	Uncharacterized protein	lipid metabolism.lipid transfer proteins etc	0.9	2.1E-02	1.6	1.5E-03	1.2	2.6E-02	0.3	ns
solyc10g075070.1.1	1	Non-specific lipid-transfer protein	lipid metabolism.lipid transfer proteins etc	0.6	6.5E-03	0.5	2.1E-02	1.1	2.7E-03	0.9	1.2E-02
solyc10g078550.1.1	1	Glutamate dehydrogenase	N-metabolism.N-degradation.glutamate dehydrogenase	2.3	2.3E-02	0.8	ns	0.5	ns	0	ns
solyc05g054050.2.1	1	Glutamate decarboxylase	amino acid metabolism.synthesis.central amino acid metabolism.GABA.Glutamate decarboxylase	1.7	5.0E-02	0.1	ns	0.8	ns	-1.9	ns
solyc08g041870.2.1	1	Aspartate aminotransferase	amino acid metabolism.synthesis.central amino acid metabolism.aspartate.aspartate aminotransferase	1	4.0E-02	0.7	5.0E-02	0.9	ns	0.7	ns
solyc01g109850.2.1	1	Uncharacterized protein	amino acid metabolism.synthesis.aspartate family.lysine.diaminopimelate decarboxylase	0.7	5.0E-02	0.4	ns	0.3	ns	-0.3	ns
solyc07g053280.2.1	1	Ketol-acid reductoisomerase	amino acid metabolism.synthesis.branched chain group.common	-0.8	ns	0.1	ns	0.5	ns	0.6	ns
solyc08g014340.2.1	1	Uncharacterized protein	amino acid metabolism.synthesis.serine-glycine-cysteine group.cysteine.OASTL	0.9	5.0E-02	-0.2	ns	-0.2	ns	-0.9	ns
solyc09g082060.2.1	1	Cysteine synthase	amino acid metabolism.synthesis.serine-glycine-cysteine group.cysteine.OASTL	1	1.8E-02	0.4	ns	0.8	ns	0.2	ns
solyc06g073280.2.1	1	Uncharacterized protein	amino acid metabolism.synthesis.aromatic aa.phenylalanine and tyrosine	1	1.1E-02	0.6	ns	0	ns	-0.1	ns
solyc09g061840.2.1	1	Uncharacterized protein	amino acid metabolism.degradation.branched-chain group.shared	1.4	3.7E-03	0.7	ns	0.1	ns	-0.3	ns
solyc03g005260.2.1	1	Uncharacterized protein	S-assimilation.ATPS	0.3	ns	-1.1	ns	-1	ns	-1	ns
solyc04g056390.2.1	1	Plastid isopentenyl diphosphate isomerase	secondary metabolism.isoprenoids.mevalonate pathway.isopentenyl pyrophosphate:dimethyllallyl pyrophosphate isomerase	0.9	ns	1.4	ns	0.7	ns	-1	ns
solyc09g065730.2.1	1	Uncharacterized protein	secondary metabolism.isoprenoids.tocopherol biosynthesis.MPBQ/MSBQ methyltransferase	0.3	ns	-0.4	ns	-0.4	ns	-0.8	ns
solyc03g005230.2.1	1	Uncharacterized protein	secondary metabolism.isoprenoids.tocopherol biosynthesis.MPBQ/MSBQ methyltransferase	0.1	ns	-0.4	ns	-0.1	ns	-0.6	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc03g025320.2.1	1	Alcohol acyl transferase	secondary metabolism.phenylpropanoids	-0.8	ns	-0.7	ns	0.6	ns	-0.5	ns
solyc07g055750.2.1	1	Uncharacterized protein	secondary metabolism.N misc.alkaloid-like	0.6	ns	0.8	ns	0.9	ns	-0.1	ns
solyc09g090430.2.1	1	Cyanate hydratase	secondary metabolism.N misc.cyanogenic glycosides	0.6	6.0E-03	0.2	ns	0.1	ns	0.3	ns
solyc12g098150.1.1	1	Uncharacterized protein	hormone metabolism.auxin.induced-regulated-responsive-activated	2.1	4.1E-03	0.4	ns	1	ns	1.1	ns
solyc01g079880.2.1	1	Uncharacterized protein	hormone metabolism.auxin.induced-regulated-responsive-activated	1.7	2.8E-02	1.3	ns	0.9	ns	0.9	ns
solyc02g085730.2.1	1	Allene oxide cyclase	hormone metabolism.jasmonate.synthesis-degradation.allene oxidase cyclase	1.4	2.7E-03	1.5	1.0E-03	1.1	3.7E-02	1.1	3.3E-02
solyc06g081980.1.1	1	Uncharacterized protein	Co-factor and vitamine metabolism	0	ns	-0.9	ns	-0.8	ns	0	ns
solyc08g069030.2.1	1	Delta-aminolevulinic acid dehydratase	tetrapyrrole synthesis.ALA dehydratase	0.5	ns	0.9	ns	-1.1	ns	0.3	ns
solyc08g080650.1.1	1	Uncharacterized protein	stress.biotic	0.6	ns	0.9	1.7E-02	-0.1	ns	-0.5	ns
solyc10g055810.1.1	1	Basic 30 kDa endochitinase	stress.biotic	-0.9	ns	0.5	ns	-0.9	ns	-0.5	ns
solyc08g080620.1.1	1	PR-5x	stress.biotic	0.5	5.1E-02	0.9	4.4E-02	-0.2	ns	-0.7	ns
solyc01g097240.2.1	1	Pathogenesis-related protein P2	stress.biotic	2	5.0E-02	0.3	ns	0.8	ns	-0.4	ns
solyc01g106620.2.1	1	PR1 protein	stress.biotic	-1.4	ns	1.5	5.0E-02	-2	1.9E-02	-0.4	ns
solyc08g080640.1.1	1	Protein NP24	stress.biotic	0.4	ns	0.9	3.9E-02	-0.3	ns	-0.7	ns
solyc10g055800.1.1	1	Uncharacterized protein	stress.biotic	-0.4	ns	0.8	2.9E-02	-0.7	ns	-0.4	ns
solyc04g011440.2.1	1	Heat shock protein 70 isoform 3	stress.abiotic.heat	0.8	1.8E-04	0.2	5.1E-02	0.3	ns	0.1	ns
solyc06g076020.2.1	1	Uncharacterized protein	stress.abiotic.heat	0.8	7.2E-05	0.2	3.5E-02	0.3	ns	0.1	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc06g036290.2.1	1	Uncharacterized protein	stress.abiotic.heat	1.4	6.1E-03	1.4	4.9E-03	1.6	7.2E-03	0.8	ns
solyc07g005820.2.1	1	Uncharacterized protein	stress.abiotic.heat	0.9	5.4E-05	0.4	1.1E-02	0.4	ns	0.1	ns
solyc01g103450.2.1	1	Uncharacterized protein	stress.abiotic.heat	-0.6	5.0E-02	-0.8	3.7E-02	-0.4	3.0E-03	-0.1	ns
solyc10g086410.2.1	1	Uncharacterized protein	stress.abiotic.heat	0.8	7.8E-05	0.3	1.8E-02	0.4	ns	0.1	ns
solyc01g099660.2.1	1	Uncharacterized protein	stress.abiotic.heat	1.6	2.5E-02	0.9	ns	0.4	ns	-0.3	ns
solyc09g010630.2.1	1	Uncharacterized protein	stress.abiotic.heat	0.7	1.4E-04	0.3	2.3E-02	0.4	ns	0.1	ns
solyc11g066060.1.1	1	Uncharacterized protein	stress.abiotic.heat	0.7	7.1E-05	0.2	1.9E-02	0.4	ns	0.1	ns
solyc08g082820.2.1	1	Uncharacterized protein	stress.abiotic.heat	1.4	5.2E-04	0.8	2.1E-02	0.8	5.1E-02	0.2	ns
solyc06g052050.2.1	1	Uncharacterized protein	stress.abiotic.heat	1.2	3.3E-03	0.7	2.8E-02	1.2	1.0E-02	0.7	ns
solyc03g082920.2.1	1	Uncharacterized protein	stress.abiotic.heat	1.5	4.7E-02	0.9	9.4E-03	0.9	4.9E-02	0.3	ns
solyc11g066100.1.1	1	Uncharacterized protein	stress.abiotic.heat	0.7	1.1E-04	0.2	3.0E-02	0.3	ns	0.2	ns
solyc06g060260.2.1	1	Uncharacterized protein	redox.ascorbate and glutathione.ascorbate	0	ns	0.6	1.7E-02	0.5	ns	0.2	ns
solyc06g005160.2.1	1	Cytosolic ascorbate peroxidase 1	redox.ascorbate and glutathione.ascorbate	1.2	8.9E-04	0.1	ns	1.2	5.5E-03	0.3	ns
solyc01g111510.2.1	1	Uncharacterized protein	redox.ascorbate and glutathione.ascorbate	0.1	ns	-1.5	ns	0.3	ns	-1	ns
solyc11g011250.1.1	1	Uncharacterized protein	redox.ascorbate and glutathione.ascorbate	0.2	4.0E-02	0	ns	0.2	ns	0.1	ns
solyc02g083620.2.1	1	Uncharacterized protein	redox.ascorbate and glutathione.ascorbate	0.9	5.5E-06	0.2	4.2E-03	0.9	1.4E-04	0.3	ns
solyc07g020860.2.1	1	Thioredoxin peroxidase 1	redox.peroxiredoxin	1	1.1E-02	0.6	5.1E-02	0.4	ns	-0.4	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc01g079820.2.1	1	Uncharacterized protein	redox.peroxiredoxin	0.3	ns	0.4	6.4E-02	0.8	5.1E-02	0.6	ns
solyc04g082460.2.1	1	Catalase	redox.dismutases and catalases	0.7	5.1E-02	0	ns	-0.3	ns	-0.3	ns
solyc11g066390.1.1	1	Superoxide dismutase [Cu-Zn]	redox.dismutases and catalases	0.9	ns	-0.2	ns	-2.2	ns	0.1	ns
solyc02g082760.2.1	1	Catalase	redox.dismutases and catalases	-0.1	ns	-0.9	ns	-0.9	5.0E-02	-0.6	ns
solyc12g094620.1.1	1	Catalase isozyme 1	redox.dismutases and catalases	0.8	1.1E-03	0.4	3.7E-02	0.2	ns	0	ns
solyc04g077970.2.1	1	Uncharacterized protein	nucleotide metabolism.salvage.phosphoribosyltransferases.aprt	2	3.5E-03	1.3	5.0E-02	0.9	ns	0.3	ns
solyc01g089970.2.1	1	Nucleoside diphosphate kinase	nucleotide metabolism.phosphotransfer and pyrophosphatases.nucleoside diphosphate kinase	-0.7	ns	0	3.6E-02	0.2	ns	0.2	ns
solyc02g080630.2.1	1	Lactoylglutathione lyase	Biodegradation of Xenobiotics.lactoylglutathione lyase	1.5	1.5E-03	1	2.3E-02	0.5	5.0E-02	0.4	ns
solyc02g092530.2.1	1	Uncharacterized protein	misc.misc2	2.2	5.0E-02	0.4	ns	-1.2	ns	-0.6	ns
solyc01g074030.2.1	1	Beta-glucosidase 01	misc.gluco-, galacto- and mannosidases	-0.2	ns	1.3	1.7E-02	0.8	ns	0.9	ns
solyc06g068860.2.1	1	Alpha-mannosidase	misc.gluco-, galacto- and mannosidases.alpha-mannosidase	1.5	5.0E-02	1.7	6.4E-05	1.1	1.1E-02	0.4	ns
solyc10g079860.1.1	1	Uncharacterized protein	misc.beta 1,3 glucan hydrolases.glucan endo-1,3-beta-glucosidase	1.2	4.0E-02	0.7	ns	1	ns	-1.7	ns
solyc01g008610.2.1	1	Uncharacterized protein	misc.beta 1,3 glucan hydrolases.glucan endo-1,3-beta-glucosidase	0.9	ns	-0.5	ns	0.5	ns	-2.5	ns
solyc12g096760.1.1	1	Uncharacterized protein	misc.oxidases - copper, flavone etc.	0	ns	1.4	2.3E-03	-0.3	ns	0.2	ns
solyc07g040750.1.1	1	Uncharacterized protein	RNA.processing.RNA helicase	1.3	6.1E-04	0.2	ns	0.2	ns	-0.5	ns
solyc07g040750.1.1	1	Uncharacterized protein	DNA.synthesis/chromatin structure	1.3	6.1E-04	0.2	ns	0.2	ns	-0.5	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc08g062800.2.1	1	Uncharacterized protein	DNA.synthesis/chromatin structure	0.7	1.8E-02	0.1	ns	0.2	ns	-0.1	ns
solyc08g062800.2.1	1	Uncharacterized protein	RNA.processing.RNA helicase	0.7	1.8E-02	0.1	ns	0.2	ns	-0.1	ns
solyc01g008960.2.1	1	AG	RNA.regulation of transcription.Argonaute	1	4.1E-03	1.7	1.7E-02	2.9	5.8E-04	2.2	ns
solyc01g104170.2.1	1	Uncharacterized protein	RNA.regulation of transcription.AtSR Transcription Factor family	0.2	ns	0.4	ns	0.1	ns	0.3	4.5E-02
solyc07g008720.2.1	1	Nascent polypeptide-associated complex subunit beta	RNA.regulation of transcription.General Transcription	1.5	6.2E-03	0.4	ns	0.4	ns	0.4	ns
solyc07g008720.2.1	1	Nascent polypeptide-associated complex subunit beta	RNA.regulation of transcription.putative transcription regulator	1.5	6.2E-03	0.4	ns	0.4	ns	0.4	ns
solyc03g025850.2.1	1	Remorin 1	RNA.regulation of transcription.unclassified	1.8	2.2E-03	0.9	5.0E-02	-0.5	ns	-1.6	ns
solyc08g061000.2.1	1	Uncharacterized protein	DNA.synthesis/chromatin structure	1.4	3.4E-02	0.6	5.0E-02	0.9	ns	-0.1	ns
solyc02g038690.1.1	1	Histone H2B	DNA.synthesis/chromatin structure.histone	1.6	3.5E-02	0.6	3.9E-04	0.5	ns	0.3	ns
solyc06g074780.1.1	1	Histone H2B	DNA.synthesis/chromatin structure.histone	1.4	6.1E-04	0.6	4.3E-02	0.5	ns	0.3	ns
solyc06g074790.1.1	1	Histone H2B.1	DNA.synthesis/chromatin structure.histone	1.4	6.1E-04	0.6	4.3E-02	0.5	ns	0.3	ns
solyc11g066430.1.1	1	Histone H2B.2	DNA.synthesis/chromatin structure.histone	1.5	5.7E-04	0.6	5.0E-02	0.5	ns	0.3	ns
solyc11g007920.1.1	1	Histone H2B	DNA.synthesis/chromatin structure.histone	1.6	3.7E-04	0.7	3.2E-02	0.5	ns	0.3	ns
solyc05g056250.2.1	1	Uncharacterized protein	protein.aa activation.aspartate-tRNA ligase	1.7	1.0E-03	1.3	6.2E-03	0.7	ns	0.4	ns
solyc06g051200.2.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.50S subunit.L3	1.1	5.1E-02	1	ns	1.4	ns	2.3	ns
solyc12g100160.1.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.50S subunit.L6	0.9	5.0E-02	1.4	5.1E-02	1.6	ns	1.6	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc04g063290.2.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S2	0.1	ns	0.2	ns	1.2	2.2E-02	0.3	ns
solyc10g078620.1.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S5	1.3	6.9E-03	0.5	ns	0.7	ns	0.1	ns
solyc12g096300.1.1	1	40S ribosomal protein S6	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S6	1.1	1.9E-02	0.4	ns	0.6	ns	0.2	ns
solyc08g006040.2.1	1	40S ribosomal protein S6	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S6	1.1	2.5E-02	0.3	ns	0.6	ns	0.2	ns
solyc04g005680.2.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S9	-0.7	ns	0.2	ns	0.9	4.5E-02	0.3	ns
solyc06g073800.2.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S11	1.8	2.8E-03	1.2	2.9E-02	0.9	ns	0.5	ns
solyc01g103800.2.1	1	40S ribosomal protein S12	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S12	0.7	4.8E-02	0.5	5.0E-02	0.5	ns	0.2	ns
solyc12g042650.1.1	1	40S ribosomal protein S12	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S12	0.8	5.1E-02	0.5	5.1E-02	0.4	ns	0.2	ns
solyc11g072260.1.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S13	0.5	5.1E-02	0.6	3.0E-02	0.7	ns	0.4	ns
solyc03g078290.2.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S18	-0.2	ns	0.7	3.5E-02	0.7	ns	0.3	ns
solyc01g096580.2.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S20	1.6	3.2E-02	0.6	5.0E-02	0.7	ns	0.6	ns
solyc06g007470.2.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S26	0	ns	1.2	5.1E-02	1.8	4.3E-02	1.6	ns
solyc06g072120.2.1	1	40S ribosomal protein SA	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.SA	0.6	2.3E-03	0.4	1.5E-02	0.4	ns	0.1	ns
solyc03g097900.2.1	1	40S ribosomal protein S3a	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S3A	0.6	4.1E-02	0.2	ns	0.4	ns	0.2	ns
solyc01g103510.2.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L3	0.8	5.1E-02	0.3	ns	0.4	ns	0.3	ns
solyc07g008370.2.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L7	1.2	5.4E-02	1.3	1.1E-02	1.3	ns	0.3	ns
solyc12g096700.1.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L9	1.5	5.2E-03	0.8	3.9E-02	0.7	ns	0.3	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc08g014550.2.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L9	1.2	1.4E-02	0.7	5.1E-02	0.7	ns	0.3	ns
solyc12g010930.1.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L11	1.2	1.2E-02	1.3	7.7E-03	1.4	1.7E-02	0.8	5.0E-02
solyc08g075700.2.1	1	60S ribosomal protein L13	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L13	0.7	5.0E-02	0.7	5.0E-02	1.1	4.2E-02	0.4	ns
solyc12g096150.1.1	1	60S ribosomal protein L13	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L13	0.7	5.1E-02	0.4	ns	0.8	ns	0.2	ns
solyc09g075150.2.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L22	2	3.3E-03	1.6	3.5E-02	1.4	ns	1.4	ns
solyc01g099830.2.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L22	1.8	6.2E-03	1.4	5.0E-02	1.5	4.5E-02	1.3	5.0E-02
solyc09g090610.2.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L23	1.2	1.4E-02	0.7	ns	0	ns	-0.1	ns
solyc09g008800.2.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L24	1.1	5.1E-02	0.5	ns	0.4	ns	-0.4	ns
solyc02g092430.1.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L26	2.1	2.4E-02	1.2	ns	0.9	ns	0.6	ns
solyc11g067100.1.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.unknown	0.1	ns	0.9	1.1E-02	1.1	1.5E-02	0.9	6.0E-02
solyc10g086010.1.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L4/L1	1.7	2.6E-02	0.6	ns	0.6	ns	-0.2	ns
solyc09g007250.2.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L4/L1	1.8	2.3E-03	1	5.1E-02	0.8	ns	0.2	ns
solyc10g084350.1.1	1	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L4/L1	1.9	2.7E-02	0.8	5.0E-02	0.7	ns	-0.2	ns
solyc06g074300.2.1	1	Ribosomal protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L10A	1.2	8.9E-02	0.5	ns	0.5	ns	0.5	ns
solyc03g112150.1.1	1	Elongation factor Tu	protein.synthesis.elongation	-0.4	ns	-0.2	ns	-0.3	9.5E-03	0	ns
solyc08g062920.2.1	1	Uncharacterized protein	protein.synthesis.elongation	0.6	1.3E-04	0.1	2.4E-02	0.2	ns	0	ns
solyc07g016150.2.1	1	Uncharacterized protein	protein.synthesis.elongation	0.5	2.9E-03	0.1	ns	0.3	ns	-0.1	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc06g071790.2.1	1	Uncharacterized protein	protein.synthesis.elongation	-0.5	ns	-0.2	ns	-0.3	2.4E-02	0	ns
solyc09g065270.2.1	1	Uncharacterized protein	protein.synthesis.release	-0.9	ns	-0.2	ns	-0.1	ns	0.4	ns
solyc01g104070.2.1	1	Uncharacterized protein	protein.targeting.nucleus	0.8	1.9E-02	-0.1	ns	-0.3	ns	-0.1	ns
solyc12g008630.1.1	1	Uncharacterized protein	protein.targeting.mitochondria	0.2	ns	0.4	3.4E-02	0.4	ns	0.3	ns
solyc02g088700.2.1	1	Uncharacterized protein	protein.targeting.mitochondria	1.7	3.3E-02	0	ns	0.5	ns	-0.2	ns
solyc08g077780.2.1	1	Uncharacterized protein	protein.postranslational modification	1.5	5.0E-02	0.9	5.0E-02	0.9	ns	1	ns
solyc12g010040.1.1	1	Leucine aminopeptidase 2, chloroplastic	protein.degradation	1.9	3.2E-05	0.8	1.1E-02	-0.2	ns	0.3	ns
solyc00g187050.2.1	1	Leucine aminopeptidase 1, chloroplastic	protein.degradation	1.8	1.1E-03	0.9	3.1E-02	-1	ns	0.6	ns
solyc08g081250.2.1	1	Uncharacterized protein	protein.degradation	0.5	ns	-0.9	ns	0.3	ns	-0.2	ns
solyc08g079840.1.1	1	Uncharacterized protein	protein.degradation.subtilases	0.8	ns	0.1	ns	0	ns	-1	ns
solyc08g079880.1.1	1	P69C protein	protein.degradation.subtilases	1.1	4.3E-03	0.3	ns	0	ns	-0.6	ns
solyc08g079900.1.1	1	Uncharacterized protein	protein.degradation.subtilases	0.8	1.6E-02	0.2	ns	-0.1	ns	-0.6	ns
solyc08g079870.1.1	1	P69B protein	protein.degradation.subtilases	0.6	5.0E-02	0	ns	0	ns	-0.6	ns
solyc06g062950.1.1	1	Uncharacterized protein	protein.degradation.subtilases	0.7	ns	1.2	5.1E-02	1.9	ns	1.2	ns
solyc07g041900.2.1	1	Cysteine proteinase 3	protein.degradation.cysteine protease	0	ns	-0.6	ns	-1	2.6E-02	-0.3	ns
solyc02g069100.2.1	1	Uncharacterized protein	protein.degradation.cysteine protease	0.8	5.1E-02	-0.9	ns	0.7	ns	0	ns
solyc12g088670.1.1	1	CYP1	protein.degradation.cysteine protease	0.3	3.1E-02	-0.1	ns	-0.2	ns	-0.2	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc01g100520.2.1	1	ATP-dependent Clp protease proteolytic subunit	protein.degradation.serine protease	1.9	5.7E-03	0.5	ns	0.7	ns	0.9	ns
solyc09g008070.2.1	1	Uncharacterized protein	protein.degradation.AAA type	0.8	4.5E-02	-0.3	ns	0.5	ns	-0.1	ns
solyc09g008070.2.1	1	Uncharacterized protein	protein.degradation.ubiquitin.proteasom	0.8	4.5E-02	-0.3	ns	0.5	ns	-0.1	ns
solyc09g008070.2.1	1	Uncharacterized protein	cell.division	0.8	4.5E-02	-0.3	ns	0.5	ns	-0.1	ns
solyc11g069720.1.1	1	Uncharacterized protein	cell.division	1.2	4.4E-02	0.1	ns	0.9	ns	-0.1	ns
solyc11g069720.1.1	1	Uncharacterized protein	protein.degradation.AAA type	1.2	4.4E-02	0.1	ns	0.9	ns	-0.1	ns
solyc11g069720.1.1	1	Uncharacterized protein	protein.degradation.ubiquitin.proteasom	1.2	4.4E-02	0.1	ns	0.9	ns	-0.1	ns
solyc06g063140.2.1	1	Uncharacterized protein	protein.degradation.ubiquitin.proteasom	2.2	3.3E-02	1.3	ns	0.7	ns	1.1	ns
solyc06g065520.2.1	1	Uncharacterized protein	protein.folding	2	3.7E-03	1.2	3.7E-02	0.6	ns	1	ns
solyc06g075010.2.1	1	Uncharacterized protein	protein.folding	0.6	1.9E-03	-0.1	ns	0	ns	0.1	ns
solyc05g053470.2.1	1	Uncharacterized protein	protein.folding	1.2	3.8E-02	1	ns	0.4	ns	-0.2	ns
solyc04g015040.2.1	1	Peptidyl-prolyl cis-trans isomerase	protein.folding	0.5	5.0E-02	0.5	2.3E-02	0	ns	0.2	ns
solyc01g028810.2.1	1	Uncharacterized protein	protein.folding	0.1	4.5E-02	-0.1	ns	-0.1	ns	0.2	ns
solyc06g009400.2.1	1	PII-like protein	signalling.in sugar and nutrient physiology	1.2	5.1E-02	1.4	3.6E-02	0.5	ns	0	ns
solyc05g023800.2.1	1	GTP-binding nuclear protein Ran1	signalling.G-proteins	1	5.0E-02	0.6	7.0E-07	0.6	2.3E-03	0.4	3.0E-02
solyc08g062660.2.1	1	Ran binding protein-1	signalling.G-proteins	1.1	5.0E-02	1.5	5.0E-02	1.2	ns	0.9	ns
solyc02g063070.2.1	1	14-3-3 protein 4	signalling.14-3-3 proteins	-1	ns	-0.4	ns	0.2	ns	-0.1	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc04g011500.2.1	1	Uncharacterized protein	cell.organisation	0.8	6.4E-04	0.2	5.0E-02	0.3	5.0E-02	0.2	ns
solyc00g017210.1.1	1	Uncharacterized protein	cell.organisation	0.7	2.1E-03	0.4	1.8E-02	0.3	ns	0.3	ns
solyc01g104770.2.1	1	Uncharacterized protein	cell.organisation	0.7	4.4E-02	0.2	ns	0.3	ns	0.3	ns
solyc11g070130.1.1	1	Profilin	cell.organisation	1.6	7.1E-03	1.1	5.0E-02	0.2	ns	0.4	ns
solyc03g078400.2.1	1	Uncharacterized protein	cell.organisation	0.6	9.7E-04	0.2	5.1E-02	0.3	ns	0.2	ns
solyc11g005330.1.1	1	Uncharacterized protein	cell.organisation	0.6	1.0E-03	0.2	4.4E-02	0.3	ns	0.2	ns
solyc04g071260.2.1	1	Uncharacterized protein	cell.organisation	0.9	1.1E-02	0.4	ns	0.3	ns	0.4	ns
solyc06g051650.2.1	1	Peptidyl-prolyl cis-trans isomerase	cell.cycle.peptidylprolyl isomerase	2.2	1.8E-04	0.7	5.0E-02	0.5	ns	0.1	ns
solyc01g111170.2.1	1	Peptidyl-prolyl cis-trans isomerase	cell.cycle.peptidylprolyl isomerase	0.6	1.9E-02	-0.2	ns	0.8	ns	0.1	ns
solyc01g100450.1.1	1	Uncharacterized protein	development.unspecified	1	2.0E-02	0.7	ns	0.4	ns	-0.4	ns
solyc09g048990.2.1	1	Uncharacterized protein	transport.p- and v-ATPases.H+-transporting two-sector ATPase	1.2	5.1E-02	0.8	ns	0.7	ns	0.5	ns
solyc12g055800.1.1	1	Uncharacterized protein	transport.p- and v-ATPases.H+-transporting two-sector ATPase	1	2.9E-04	0.5	9.9E-03	0.8	2.9E-02	0.2	ns
solyc07g005940.2.1	1	Uncharacterized protein	transport.p- and v-ATPases.H+-transporting two-sector ATPase.subunit H	-0.2	ns	0.5	ns	1.1	5.0E-02	0.4	ns
solyc01g010760.2.1	1	Uncharacterized protein	transport.sugars	1.2	2.4E-04	0.5	ns	-0.2	ns	-0.4	ns
solyc05g051560.2.1	1	Uncharacterized protein	transport.metabolite transporters at the mitochondrial membrane	1.2	ns	0.8	ns	0.7	ns	0.5	ns
solyc03g044050.1.1	1	Uncharacterized protein	not assigned.unknown	0.3	ns	-0.5	ns	-0.4	ns	0	ns
solyc06g007340.2.1	1	Uncharacterized protein	not assigned.unknown	0.1	ns	0.8	1.8E-03	0.9	1.2E-02	0.6	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc11g027870.1.1	1	Uncharacterized protein	not assigned.unknown	1	ns	0.6	5.0E-02	0.7	ns	0	ns
solyc11g068510.1.1	1	Uncharacterized protein	not assigned.unknown	1.3	1.4E-04	0.3	ns	0.1	ns	0	ns
solyc04g054980.2.1	1	Uncharacterized protein	not assigned.unknown	0.5	2.8E-02	0.8	4.0E-03	0.8	3.1E-02	0.5	ns
solyc01g006900.2.1	1	Uncharacterized protein	not assigned.unknown	1.1	9.3E-04	0.7	3.0E-02	0.6	ns	0.2	ns
solyc12g049090.1.1	1	Uncharacterized protein	not assigned.unknown	-0.2	ns	-0.5	ns	-0.5	ns	-0.3	ns
solyc09g092380.2.1	1	Adenosylhomocysteinase	not assigned.unknown	0	ns	-0.8	ns	0.3	ns	0.1	ns
solyc06g062280.2.1	1	Uncharacterized protein	not assigned.unknown	1.9	3.2E-04	0.7	5.0E-02	0.7	ns	0.6	ns
solyc07g008100.2.1	1	Uncharacterized protein	not assigned.unknown	0.4	ns	0.8	3.3E-02	0.3	ns	0.3	ns
solyc02g083500.2.1	1	Uncharacterized protein	not assigned.unknown	1.2	6.2E-03	-0.4	ns	0.3	ns	0	ns
solyc02g089080.2.1	1	Uncharacterized protein	not assigned.unknown	0.3	ns	0.7	ns	0	ns	-1.7	ns
solyc08g074630.1.1	1	Uncharacterized protein	not assigned.unknown	-0.4	ns	0.9	ns	-0.7	ns	1.4	ns
solyc03g063240.2.1	1	Uncharacterized protein	not assigned.unknown	1.2	ns	-0.7	ns	-0.7	ns	-0.1	ns
solyc01g010100.1.1	1	Uncharacterized protein	not assigned.unknown	0.6	5.1E-02	0.1	ns	-0.3	ns	-0.4	ns
solyc08g081880.1.1	1	Uncharacterized protein	not assigned.unknown	-0.4	ns	-0.8	2.5E-02	-0.5	4.4E-03	-0.1	ns
solyc04g055340.2.1	1	Uncharacterized protein	not assigned.unknown	1.4	3.8E-02	0.7	1.2E-03	0.6	3.0E-01	0.7	ns
solyc05g005460.2.1	1	Uncharacterized protein	not assigned.unknown	1.2	1.4E-03	0.6	ns	0.4	ns	0.3	ns
solyc01g098380.2.1	2	Uncharacterized protein	amino acid metabolism.synthesis.aspartate family.lysine.dihydrodipicolinate reductase	4.6	1.1E-02	3.9	7.7E-03	-10	ns	0.9	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc08g075490.2.1	2	Uncharacterized protein	hormone metabolism.abscisic acid.synthesis-degradation.synthesis.9-cis-epoxycarotenoid dioxygenase	-10	5.0E-02	-10	4.9E-02	-10	ns	1.4	ns
solyc05g056160.2.1	2	Proteasome subunit beta type	protein.degradation.ubiquitin.proteasom	3.7	5.0E-02	0.6	ns	-10	ns	-0.2	ns
solyc08g008630.2.1	2	Uncharacterized protein	not assigned.unknown	9.9	1.4E-03	-10	ns	-10	ns	0.9	ns
solyc03g115900.2.1	3	Uncharacterized protein	PS.lightreaction.photosystem II.LHC-II	-2.7	5.1E-02	-2.3	ns	-0.5	ns	-0.3	ns
solyc02g065400.2.1	3	Oxygen-evolving enhancer protein 1, chloroplastic	PS.lightreaction.photosystem II.PSII polypeptide subunits	-1.1	1.2E-02	-0.7	5.0E-02	-0.6	1.8E-02	-0.1	ns
solyc02g090030.2.1	3	Uncharacterized protein	PS.lightreaction.photosystem II.PSII polypeptide subunits	-1.3	4.0E-02	-0.9	5.0E-02	-0.6	9.5E-03	-0.1	ns
solyc08g013670.2.1	3	Uncharacterized protein	PS.lightreaction.photosystem I.PSI polypeptide subunits	-1.6	2.4E-03	-1.2	3.3E-02	-0.5	ns	-0.1	ns
solyc09g063130.2.1	3	Uncharacterized protein	PS.lightreaction.photosystem I.PSI polypeptide subunits	-1.6	4.6E-03	-1	ns	-0.4	ns	0	ns
solyc06g066000.1.1	3	Uncharacterized protein	PS.lightreaction.ATP synthase	-0.9	3.6E-02	-1	4.5E-03	-0.4	6.8E-03	-0.1	ns
solyc06g065990.1.1	3	Uncharacterized protein	PS.lightreaction.ATP synthase	-0.9	1.3E-02	-0.9	1.0E-02	-0.4	4.2E-02	-0.1	ns
solyc10g044540.1.1	3	Uncharacterized protein	PS.lightreaction.ATP synthase.alpha subunit	-2.3	1.9E-05	-1.7	4.0E-04	-0.6	ns	-0.1	ns
solyc02g080540.1.1	3	Uncharacterized protein	PS.lightreaction.ATP synthase.gamma chain	-1	4.4E-02	-1.3	3.7E-03	-0.7	1.8E-02	-0.3	ns
solyc08g083360.2.1	3	Uncharacterized protein	PS.lightreaction.other electron carrier (ox/red).ferredoxin	-0.3	ns	-2	4.7E-02	-1	ns	-0.8	ns
solyc10g075160.1.1	3	Uncharacterized protein	PS.lightreaction.other electron carrier (ox/red).ferredoxin	-2.2	8.3E-03	-2.2	6.4E-03	-0.4	ns	0.4	ns
solyc02g083810.2.1	3	Ferredoxin--NADP reductase	PS.lightreaction.other electron carrier (ox/red).ferredoxin reductase	-0.8	4.4E-02	-0.7	ns	-0.4	7.2E-03	0	ns
solyc02g062130.2.1	3	Uncharacterized protein	PS.lightreaction.other electron carrier (ox/red).ferredoxin reductase	-1.5	1.1E-02	-1.2	4.2E-05	-0.5	6.4E-04	-0.2	ns
solyc04g057980.2.1	3	Uncharacterized protein	PS.lightreaction.NADH DH	-3.7	4.0E-02	-2.5	ns	-2	ns	-1	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6hom o/MM fold	T6hom o/MM_ P val	T19ho mo/M M_fold	T19ho mo/MM _P val	T6hem i/MM_ fold	T6hem i/MM_ P val	T19he mi/M M_fold	T19he mi/MM _P val
solyc08g08 0050.2.1	3	Uncharacterized protein	PS.lightreaction.cyclic electron flow-chlororespiration	-1.7	7.4E-03	-1.7	4.7E-03	-0.9	3.4E-02	-0.2	ns
solyc02g08 0280.1.1	3	NAD(P)H-quinone oxidoreductase subunit 1, chloroplastic	PS.lightreaction.cyclic electron flow-chlororespiration	-3.5	5.0E-02	-4.9	5.1E-02	-1.6	ns	-2.8	ns
solyc11g00 8620.1.1	3	Uncharacterized protein	PS.photorespiration.phosphoglycolate phosphatase	-1.5	7.7E-05	-0.9	ns	-0.5	2.0E-02	-0.1	ns
solyc10g00 7600.2.1	3	Uncharacterized protein	PS.photorespiration.glycolate oxydase	-2.1	3.3E-05	-2.5	3.0E-06	-1	1.7E-03	-0.4	ns
solyc07g05 6540.2.1	3	Uncharacterized protein	PS.photorespiration.glycolate oxydase	-1.8	3.7E-04	-2.1	4.7E-05	-1	3.5E-03	-0.4	ns
solyc08g04 8250.2.1	3	Uncharacterized protein	PS.photorespiration.glycolate oxydase	-1.7	3.0E-04	-2	4.7E-05	-0.8	4.9E-03	-0.1	ns
solyc12g09 9930.1.1	3	Hop-interacting protein THI032	PS.photorespiration.aminotransferases peroxisomal	-1.8	2.9E-02	-2.4	2.1E-02	-1.2	ns	-0.8	ns
solyc02g09 1560.2.1	3	Serine hydroxymethyltransferase	PS.photorespiration.serine hydroxymethyltransferase	-1.7	2.0E-04	-1.9	2.9E-05	-0.9	2.9E-03	-0.2	ns
solyc01g11 1630.2.1	3	Uncharacterized protein	PS.photorespiration.hydroxypyruvate reductase	-1.2	5.1E-03	-1.9	8.9E-05	-1.2	4.2E-04	-0.5	ns
solyc01g00 7330.2.1	3	Ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (Fragment)	PS.calvin cycle.rubisco large subunit	-1.2	3.7E-02	-1.2	5.1E-02	-0.7	ns	-0.1	ns
solyc02g06 3150.2.1	3	Ribulose bisphosphate carboxylase small chain 1, chloroplastic	PS.calvin cycle.rubisco small subunit	-1.2	3.7E-02	-1.2	5.1E-02	-0.7	ns	-0.2	ns
solyc02g08 5950.2.1	3	Ribulose bisphosphate carboxylase small chain 3B, chloroplastic	PS.calvin cycle.rubisco small subunit	-1.3	3.0E-02	-1.2	5.0E-02	-0.6	ns	-0.1	ns
solyc07g06 6600.2.1	3	Phosphoglycerate kinase	PS.calvin cycle.phosphoglycerate kinase	-1.7	2.4E-04	-1.1	5.1E-02	-0.3	ns	-0.1	ns
solyc07g06 6610.2.1	3	Phosphoglycerate kinase	PS.calvin cycle.phosphoglycerate kinase	-1.7	5.0E-02	-1.4	1.5E-03	-0.5	5.8E-05	-0.2	ns
solyc12g09 4640.1.1	3	Glyceraldehyde-3-phosphate dehydrogenase	PS.calvin cycle.GAP	-1.4	9.1E-04	-1.6	3.9E-04	-0.7	5.2E-03	-0.2	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc04g009030.2.1	3	Glyceraldehyde-3-phosphate dehydrogenase	PS.calvin cycle.GAP	-1.4	3.2E-03	-1.5	1.4E-03	-0.6	3.5E-02	-0.2	ns
solyc04g082630.2.1	3	Glyceraldehyde-3-phosphate dehydrogenase	PS.calvin cycle.GAP	-1.4	1.7E-03	-1.5	7.4E-04	-0.7	5.7E-03	-0.2	ns
solyc02g020940.2.1	3	Glyceraldehyde-3-phosphate dehydrogenase	PS.calvin cycle.GAP	-1.6	1.1E-03	-1.6	5.6E-04	-0.7	1.8E-02	-0.3	ns
solyc07g005390.2.1	3	Uncharacterized protein	PS.calvin cycle.GAP	-1.9	3.1E-04	-1.5	3.2E-03	-0.3	ns	0	ns
solyc01g111120.2.1	3	Triosephosphate isomerase	PS.calvin cycle.TPI	-1.2	ns	-1.5	5.0E-02	-0.4	ns	-0.4	ns
solyc10g054870.1.1	3	Triosephosphate isomerase	PS.calvin cycle.TPI	-0.7	ns	-1.1	2.0E-04	-0.7	7.3E-04	-0.1	ns
solyc01g110360.2.1	3	Fructose-bisphosphate aldolase	PS.calvin cycle.aldolase	-0.5	ns	-0.9	2.3E-02	-0.5	1.0E-02	0	ns
solyc07g065900.2.1	3	Fructose-bisphosphate aldolase	PS.calvin cycle.aldolase	-1.3	8.6E-03	-1.8	2.4E-04	-1	1.5E-03	-0.1	ns
solyc05g008600.2.1	3	Fructose-bisphosphate aldolase	PS.calvin cycle.aldolase	-0.8	1.3E-02	-0.9	5.8E-03	-0.5	1.4E-03	0	ns
solyc12g056530.1.1	3	Uncharacterized protein	PS.calvin cycle.FBPase	-3.3	3.1E-04	-3.1	2.2E-04	-1.7	1.3E-02	-0.3	ns
solyc04g071340.2.1	3	Uncharacterized protein	PS.calvin cycle.FBPase	-3.3	3.3E-04	-3.1	2.5E-04	-1.7	1.5E-02	-0.2	ns
solyc10g018300.1.1	3	Uncharacterized protein	PS.calvin cycle.transketolase	-1.4	4.2E-05	-1.4	4.6E-05	-0.6	3.4E-03	-0.3	ns
solyc05g050970.2.1	3	Uncharacterized protein	PS.calvin cycle.transketolase	-1	1.4E-02	-1.2	2.3E-03	-0.6	8.9E-03	-0.3	ns
solyc05g052600.2.1	3	Chloroplast sedoheptulose-1,7-bisphosphatase	PS.calvin cycle.seduheptulose bisphosphatase	-1.2	4.1E-05	-1.3	3.5E-05	-0.6	3.7E-04	-0.2	ns
solyc08g076220.2.1	3	Phosphoribulokinase	PS.calvin cycle.PRK	-0.9	3.3E-03	-1.1	7.9E-05	-0.6	3.9E-04	-0.2	ns
solyc09g011080.2.1	3	Uncharacterized protein	PS.calvin cycle.rubisco interacting	-1.6	6.0E-03	-1.9	1.4E-03	-0.9	1.7E-02	-0.2	ns
solyc10g086580.1.1	3	Uncharacterized protein	PS.calvin cycle.rubisco interacting	-1.8	7.7E-03	-1.8	9.2E-04	-1	7.4E-04	-0.1	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc01g079790.2.1	3	Glucose-1-phosphate adenylyltransferase	major CHO metabolism.synthesis.starch.AGPase	-1.6	1.8E-02	-1.6	4.1E-02	-0.5	ns	0	ns
solyc04g015150.2.1	3	Uncharacterized protein	minor CHO metabolism.misc	-1.3	3.9E-04	-0.8	5.0E-02	-0.4	ns	-0.1	ns
solyc05g014470.2.1	3	Glyceraldehyde-3-phosphate dehydrogenase	glycolysis.cytosolic branch.glyceraldehyde 3-phosphate dehydrogenase (GAP-DH)	-1	3.5E-02	-0.6	ns	-0.3	ns	0.1	ns
solyc03g111010.2.1	3	Glyceraldehyde-3-phosphate dehydrogenase	glycolysis.cytosolic branch.glyceraldehyde 3-phosphate dehydrogenase (GAP-DH)	-1.3	3.5E-03	-0.7	ns	-0.3	ns	0.1	ns
solyc03g114500.2.1	3	Uncharacterized protein	glycolysis.cytosolic branch.enolase	-1.8	3.7E-04	-1.1	5.0E-02	-0.6	ns	-0.3	ns
solyc05g026490.2.1	3	Uncharacterized protein	glycolysis.plastid branch.phosphoglucomutase (PGM)	-3	5.2E-03	-3.8	6.2E-04	-2.6	3.3E-03	-1.3	ns
solyc05g054060.2.1	3	Uncharacterized protein	glycolysis.unclear/dually targeted.UGPase	-1.7	5.0E-02	-1.7	5.0E-02	-0.7	ns	-0.6	ns
solyc11g011960.1.1	3	Uncharacterized protein	glycolysis.unclear/dually targeted.UGPase	-2.2	1.4E-04	-2.2	1.5E-04	-0.6	ns	-0.4	ns
solyc02g063490.2.1	3	Malate dehydrogenase	gluconeogenesis.Malate DH	-1.1	ns	-1.9	6.1E-03	-0.5	ns	-0.4	ns
solyc01g097460.2.1	3	Uncharacterized protein	OPP.non-reductive PP.ribose 5-phosphate isomerase	-0.5	ns	-1.2	3.3E-02	-0.5	ns	-0.3	ns
solyc12g099100.1.1	3	Dihydrolipoyl dehydrogenase	TCA / org. transformation.TCA.pyruvate DH.E3	-1.1	3.9E-02	-1.4	2.6E-03	-0.5	ns	-0.2	ns
solyc05g053300.2.1	3	Dihydrolipoyl dehydrogenase	TCA / org. transformation.TCA.pyruvate DH.E3	-1.4	1.9E-03	-2	4.8E-05	-0.7	2.1E-02	-0.3	ns
solyc05g050120.2.1	3	Malic enzyme	TCA / org. transformation.other organic acid transformaitons.malic	-1.4	2.9E-02	-0.9	ns	-1.1	3.9E-02	0	ns
solyc05g005490.2.1	3	Carbonic anhydrase	TCA / org. transformation.carbonic anhydrases	-1.4	ns	-4	5.0E-02	-1.4	ns	0	ns
solyc02g086820.2.1	3	Carbonic anhydrase	TCA / org. transformation.carbonic anhydrases	-2.6	2.1E-03	-2.9	7.0E-04	-1.3	2.4E-02	0	ns
solyc01g007320.2.1	3	ATP synthase subunit beta, chloroplastic	mitochondrial electron transport / ATP synthesis.F1-ATPase	-0.7	ns	-1.1	3.6E-03	-0.4	3.4E-02	-0.3	ns
solyc09g082990.2.1	3	GDP-mannose 3',5'-epimerase	cell wall.precursor synthesis.UXS	-1.1	5.4E-02	-1.6	3.1E-02	-1	ns	-0.2	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6hom o/MM fold	T6hom o/MM_ P val	T19ho mo/M M_fold	T19ho mo/MM _P val	T6hem i/MM_ fold	T6hem i/MM_ P val	T19he mi/M M_fold	T19he mi/MM _P val
solyc02g08 0210.2.1	3	Pectinesterase	cell wall.pectin*esterases.PME	-1.2	ns	-1.6	5.1E-02	-1.2	ns	0.5	ns
solyc03g06 3560.2.1	3	Uncharacterized protein	N-metabolism.ammonia metabolism.glutamate synthase	-1.5	1.8E-04	-1	3.0E-02	-0.5	4.3E-02	-0.2	ns
solyc11g01 1380.1.1	3	Glutamine synthetase	N-metabolism.ammonia metabolism.glutamine synthase	-2.5	5.0E-02	-2.9	1.9E-02	0.7	ns	-1	ns
solyc01g08 0280.2.1	3	Glutamine synthetase	N-metabolism.ammonia metabolism.glutamine synthase	-0.4	ns	-1	5.0E-02	-0.5	ns	-0.2	ns
solyc05g01 3380.2.1	3	Uncharacterized protein	amino acid metabolism.synthesis.central amino acid metabolism.alanine.alanine aminotransferase	-1.9	1.1E-02	-2.9	1.4E-04	-1.4	2.0E-02	-0.7	ns
solyc01g00 7940.2.1	3	Uncharacterized protein	amino acid metabolism.synthesis.central amino acid metabolism.alanine.alanine aminotransferase	-2.5	2.2E-03	-3.3	1.1E-04	-1.4	4.6E-02	-0.7	ns
solyc12g09 9930.1.1	3	Hop-interacting protein THI032	amino acid metabolism.synthesis.central amino acid metabolism.alanine.alanine-glyoxylate aminotransferase	-1.8	2.9E-02	-2.4	2.1E-02	-1.2	ns	-0.8	ns
solyc08g06 5220.2.1	3	Uncharacterized protein	amino acid metabolism.degradation.serine-glycine-cysteine group.glycine	-1.5	1.1E-02	-2.3	2.8E-04	-0.8	ns	-0.2	ns
solyc02g08 0810.2.1	3	Aminomethyltransferase	amino acid metabolism.degradation.serine-glycine-cysteine group.glycine	-2.2	5.2E-04	-2.3	2.6E-04	-0.9	4.7E-02	-0.3	ns
solyc03g11 4340.2.1	3	Uncharacterized protein	secondary metabolism.isoprenoids.non-mevalonate pathway.DXR	-1.4	5.0E-02	-0.4	ns	-1.2	4.4E-02	-0.1	ns
solyc01g00 8550.2.1	3	Phenylacetaldehyde reductase	secondary metabolism.flavonoids.dihydroflavonols	-2.6	1.2E-02	-2	4.8E-02	-0.9	ns	-0.4	ns
solyc11g06 9800.1.1	3	Allene oxide synthase	hormone metabolism.jasmonate.synthesis-degradation.allene oxidase synthase	-0.8	4.8E-02	-1.2	5.6E-03	-0.6	3.0E-02	-0.1	ns
solyc03g11 1610.2.1	3	Uncharacterized protein	Co-factor and vitamine metabolism.riboflavin	-2.2	1.6E-02	-1.6	5.0E-02	-0.4	ns	-0.1	ns
solyc03g11 8240.2.1	3	Uncharacterized protein	tetrapyrrole synthesis.magnesium protoporphyrin IX methyltransferase	-3.7	2.2E-02	-3.3	2.7E-02	-0.8	ns	-0.5	ns
solyc12g01 3710.1.1	3	Uncharacterized protein	tetrapyrrole synthesis.protochlorophyllide reductase	0.2	ns	-1.5	ns	0.6	ns	1.6	ns
solyc04g05 0950.2.1	3	Uncharacterized protein	stress.abiotic.unspecified	-0.8	ns	-1.1	5.1E-02	-0.6	ns	0.2	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6hom o/MM fold	T6hom o/MM_ P val	T19ho mo/M M_fold	T19ho mo/MM _P val	T6hem i/MM_ fold	T6hem i/MM_ P val	T19he mi/M M_fold	T19he mi/MM _P val
solyc04g08 1970.2.1	3	Uncharacterized protein	redox.thioredoxin	-1.9	5.0E-02	-1.8	ns	-0.4	ns	0.2	ns
solyc04g07 4640.2.1	3	Uncharacterized protein	redox.ascorbate and glutathione.ascorbate	-1.4	6.5E-04	-0.8	5.1E-02	-0.6	2.2E-02	-0.1	ns
solyc05g05 3300.2.1	3	Dihydrolipoyl dehydrogenase	redox.ascorbate and glutathione.glutathione	-1.4	1.9E-03	-2	4.8E-05	-0.7	2.1E-02	-0.3	ns
solyc07g04 2440.2.1	3	Uncharacterized protein	redox.peroxiredoxin	-1.8	7.4E-04	-1.3	3.8E-02	-0.4	ns	-0.1	ns
solyc01g10 6430.2.1	3	Uncharacterized protein	nucleotide metabolism.phosphotransfer and pyrophosphatases.misc	-0.9	5.1E-02	-0.6	ns	-0.3	ns	0	ns
solyc05g05 3810.2.1	3	Serine hydroxymethyltransferase	C1-metabolism.glycine hydroxymethyltransferase	-0.7	ns	-1.6	1.8E-02	-0.5	ns	-0.3	ns
solyc01g10 7820.2.1	3	Uncharacterized protein	misc.UDP glucosyl and glucoronyl transferases	2	ns	-10	8.8E-04	-0.4	ns	-0.8	ns
solyc05g00 5480.2.1	3	2-methylene-furan-3-one reductase	misc.oxidases - copper, flavone etc.	-2.3	1.1E-03	-2.2	6.5E-04	-0.6	ns	-0.1	ns
solyc07g05 6470.2.1	3	Uncharacterized protein	misc.glutathione S transferases	-2.5	4.9E-02	-2	ns	-0.3	ns	0	ns
solyc01g07 3640.2.1	3	Putative alcohol dehydrogenase	misc.short chain dehydrogenase/reductase (SDR)	-1.6	2.3E-02	-1.1	ns	-0.8	ns	-0.2	ns
solyc03g11 4450.2.1	3	Uncharacterized protein	misc.rhodanese	-1.2	5.0E-02	-0.9	ns	-0.2	ns	0	ns
solyc11g04 2640.1.1	3	Uncharacterized protein	misc. other Ferredoxins and Rieske domain	-1.6	5.7E-03	-2	5.1E-04	-0.4	ns	-0.1	ns
solyc07g06 4600.2.1	3	Inducible plastid-lipid associated protein	RNA.processing.ribonucleases	-1.5	7.9E-03	-1.3	ns	-0.8	ns	-0.4	ns
solyc02g08 6750.1.1	3	Uncharacterized protein	RNA.regulation of transcription.PWWP domain protein	-2.6	3.1E-04	-1.8	1.0E-02	-0.9	ns	0	ns
solyc09g06 5180.2.1	3	Uncharacterized protein	RNA.regulation of transcription.unclassified	-0.9	5.0E-02	-1.1	8.7E-03	-0.6	2.8E-02	0.1	ns
solyc06g07 3260.2.1	3	Uncharacterized protein	RNA.regulation of transcription.unclassified	-1.2	2.5E-03	-1.4	2.7E-04	-0.5	3.2E-02	-0.3	ns
solyc03g11 1840.2.1	3	Uncharacterized protein	RNA.RNA binding	-1.4	3.0E-03	-0.9	ns	-0.3	ns	-0.3	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc02g077990.2.1	3	Uncharacterized protein	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.30S subunit.S5	-0.3	ns	-0.9	9.0E-03	-0.7	ns	0.1	ns
solyc10g006030.2.1	3	Uncharacterized protein	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.30S subunit.S10	-2.7	1.2E-02	-2	4.2E-02	-1	ns	-0.2	ns
solyc07g062870.2.1	3	Uncharacterized protein	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.30S subunit.S20	-1.8	2.4E-02	-1.6	5.0E-02	-0.6	ns	0	ns
solyc08g083350.2.1	3	Uncharacterized protein	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.50S subunit.L11	-4.1	4.9E-02	-4.3	4.9E-02	-1.4	ns	-1	ns
solyc03g097950.2.1	3	Uncharacterized protein	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.50S subunit.L29	-4.2	ns	-4.5	3.3E-02	-1.2	ns	-0.3	ns
solyc01g057830.2.1	3	Uncharacterized protein	protein.synthesis.ribosomal protein.prokaryotic.unknown organellar.30S subunit.S1	-1.5	2.5E-02	-1	ns	-0.4	ns	0.2	ns
solyc03g119360.2.1	3	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S7	-0.9	ns	-0.8	ns	0.4	ns	0.6	ns
solyc02g069850.2.1	3	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S25	-1.4	5.1E-02	-1.1	ns	0.3	2.8E-02	0.3	ns
solyc06g084580.1.1	3	Uncharacterized protein	protein.postranslational modification	-2.8	2.1E-03	-2.5	7.8E-04	-1.1	ns	0.2	ns
solyc06g050270.1.1	3	Non-specific serine/threonine protein kinase	protein.postranslational modification	-0.9	ns	-1.2	2.2E-02	-0.6	3.5E-02	-0.1	ns
solyc02g071180.2.1	3	Uncharacterized protein	protein.postranslational modification	-1.4	4.9E-02	-1	ns	-0.3	ns	0.2	ns
solyc01g087740.1.1	3	Uncharacterized protein	protein.degradation.subtilases	-1.5	ns	-0.5	ns	-2.1	2.8E-03	-0.9	ns
solyc01g087780.2.1	3	Subtilisin-like protease	protein.degradation.subtilases	-1.5	5.0E-02	-0.5	ns	-2.1	2.8E-03	-0.9	ns
solyc04g082250.2.1	3	FtsH-like protein	protein.degradation.metalloprotease	-1.7	5.8E-05	-1.1	1.2E-02	-0.5	ns	-0.1	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc05g007470.2.1	3	Uncharacterized protein	protein.degradation.AAA type	-0.4	ns	-1.2	5.0E-02	-0.5	ns	-0.3	ns
solyc12g098940.1.1	3	Uncharacterized protein	protein.degradation.ubiquitin.ubiquitin	-1.1	9.3E-02	-1	ns	0.2	ns	-0.1	ns
solyc04g074230.2.1	3	14-3-3 protein 7	signalling.14-3-3 proteins	-1.9	2.2E-02	-1.6	5.1E-02	0.2	ns	0.2	ns
solyc01g010360.2.1	3	Uncharacterized protein	signalling.14-3-3 proteins	-1.1	5.0E-02	-0.9	5.0E-02	0.2	ns	-0.1	ns
solyc07g053260.2.1	3	14-3-3 protein 9	signalling.14-3-3 proteins	-1.2	4.8E-02	-1	ns	0.2	ns	-0.1	ns
solyc10g051110.1.1	3	Uncharacterized protein	signalling.light	-1	ns	-1.1	ns	-0.7	ns	0.4	ns
solyc07g063120.2.1	3	Uncharacterized protein	signalling.light	-2.8	4.0E-02	-2.5	2.1E-03	-1.1	7.8E-04	0.2	ns
solyc03g113400.2.1	3	Plasma membrane ATPase 1	transport.p- and v-ATPases	-2.1	1.9E-03	-1.8	9.8E-03	-0.2	ns	-0.6	ns
solyc06g071100.2.1	3	Plasma membrane ATPase 2	transport.p- and v-ATPases	-1.4	4.8E-02	-1.4	5.0E-02	-0.1	ns	-0.5	ns
solyc01g005620.2.1	3	Uncharacterized protein	transport.metabolite transporters at the mitochondrial membrane	-2.6	8.1E-03	-2.4	1.5E-02	-1	ns	-0.6	ns
solyc04g051580.2.1	3	Uncharacterized protein	transport.metabolite transporters at the mitochondrial membrane	-2.1	5.9E-03	-2.2	1.6E-03	-1.2	3.4E-02	-0.4	ns
solyc12g099650.1.1	3	Uncharacterized protein	not assigned.unknown	-2	2.0E-02	-1.6	5.0E-02	-0.9	ns	-0.3	ns
solyc10g007290.2.1	3	Uncharacterized protein	not assigned.unknown	-1.1	ns	-0.7	ns	0.3	ns	0.3	ns
solyc01g005520.2.1	3	Uncharacterized protein	not assigned.unknown	-1.1	ns	-0.8	ns	-0.6	ns	0.2	ns
solyc11g045160.1.1	3	Uncharacterized protein	not assigned.unknown	-1.5	ns	-4.4	5.1E-02	-1.1	ns	-0.7	ns
solyc12g005090.1.1	3	Uncharacterized protein	not assigned.unknown	-1.7	5.7E-03	-1.9	2.5E-03	-0.6	ns	-0.2	ns
solyc01g066970.2.1	3	Uncharacterized protein	not assigned.unknown	-1.4	ns	-2.6	9.7E-03	-0.9	ns	-0.3	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc01g088020.2.1	3	Uncharacterized protein	not assigned.unknown	-0.2	ns	-2.3	ns	0.8	ns	1	ns
solyc03g113800.2.1	4	Uncharacterized protein	fermentation.aldehyde dehydrogenase	5.6	ns	5.7	ns	2.5	ns	-10	ns
solyc10g008110.2.1	4	Acyl-coenzyme A oxidase	lipid metabolism.lipid degradation.beta-oxidation.acyl CoA DH	3.5	5.1E-02	-1.1	ns	-2.4	ns	-10	ns
solyc11g073160.1.1	4	Uncharacterized protein	Co-factor and vitamine metabolism.riboflavin.GTP cyclohydrolase II	9.6	4.4E-02	7.4	5.0E-02	3	ns	-6.1	ns
solyc02g076720.2.1	4	Uncharacterized protein	nucleotide metabolism.synthesis.purine.FGAR amidotransferase	9.2	5.8E-03	7.5	1.5E-02	4.4	ns	-10	ns
solyc03g006700.2.1	4	Peroxidase	misc.peroxidases	7.2	1.8E-02	5.2	2.9E-02	3.4	ns	-10	ns
solyc01g105710.2.1	4	Peptidyl-prolyl cis-trans isomerase	protein.folding	9.6	4.4E-02	7.4	5.0E-02	3	ns	-6.1	ns
solyc11g066440.1.1	4	Uncharacterized protein	cell.cell death.plants	4.6	5.0E-02	4.9	5.0E-02	2.2	ns	-10	ns
solyc09g014450.2.1	4	Uncharacterized protein	not assigned.unknown	9.6	4.4E-02	7.4	5.0E-02	3	ns	-6.1	ns
solyc07g063040.2.1	5	Probable bifunctional methylthioribulose-1-phosphate dehydratase/enolase-phosphatase E1	minor CHO metabolism.others	-4.8	5.1E-02	-10	1.2E-02	-1.5	ns	-1.6	ns
solyc05g056490.2.1	5	Uncharacterized protein	nucleotide metabolism.degradation	-3.2	ns	-10	9.1E-03	-0.6	ns	-1	ns
solyc03g025410.2.1	5	Uncharacterized protein	misc.short chain dehydrogenase/reductase (SDR)	-10	4.9E-04	-10	4.9E-04	-1.4	ns	-0.2	ns
solyc02g069260.2.1	5	Protein argonaute	RNA.regulation of transcription.Argonaute	-7.6	1.5E-02	-4.8	2.4E-02	0.2	ns	0.3	ns
solyc04g080630.2.1	5	50S ribosomal protein L31	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.50S subunit.L31	-10	1.0E-02	-10	1.0E-02	-3.8	3.5E-02	-1	ns
solyc09g091740.2.1	5	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L13A	-10	5.1E-02	-10	5.1E-02	-0.6	ns	-0.2	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc05g014760.2.1	5	Uncharacterized protein	protein.postranslational modification	-10	ns	-10	ns	1.3	ns	-10	ns
solyc02g086270.2.1	5	Uncharacterized protein	protein.postranslational modification.kinase.receptor like cytoplasmatic kinase VII	-10	2.0E-04	-10	ns	-3.1	ns	-0.4	ns
solyc10g011770.2.1	5	Uncharacterized protein	protein.degradation	-7.5	1.4E-06	-5.4	6.4E-05	-0.2	ns	0.4	ns
solyc07g041920.2.1	5	Uncharacterized protein	protein.degradation.cysteine protease	-7	3.3E-02	-4.8	7.8E-04	-2.5	1.6E-05	-0.5	ns
solyc10g084110.1.1	5	Uncharacterized protein	signalling.receptor kinases.DUF 26	-10	5.0E-02	-10	5.0E-02	-3.1	ns	-0.4	ns
solyc01g105810.2.1	5	GDP dissociation inhibitor (Fragment)	signalling.G-proteins	-10	ns	-10	ns	1.6	6.7E-03	-10	ns
solyc01g080240.2.1	5	Mitogen-activated protein kinase	signalling.MAP kinases	-10	ns	-10	ns	1.3	ns	-10	ns
solyc01g009080.2.1	5	Uncharacterized protein	not assigned.unknown	-3	5.0E-02	-10	5.0E-02	-2.6	ns	-0.6	ns
solyc07g066310.2.1	6	Photosystem II 10 kDa polypeptide, chloroplastic	PS.lightreaction.photosystem II.PSII polypeptide subunits	-6.7	7.1E-05	-2.5	4.3E-03	-0.8	ns	0	ns
solyc05g007780.2.1	6	Uncharacterized protein	PS.lightreaction.photosystem II.PSII polypeptide subunits	-10	3.9E-04	-3.4	9.5E-03	-0.4	ns	-1	ns
solyc10g005050.2.1	6	Uncharacterized protein	PS.lightreaction.photosystem I.PSI polypeptide subunits	-9.1	1.1E-04	-5	1.7E-03	-1.5	ns	0.2	ns
solyc01g007540.2.1	6	Cytochrome b6-f complex subunit 4	PS.lightreaction.cytochrome b6/f.subunit 4 (PETD)	-10	1.4E-04	-8.1	2.4E-03	-1.6	ns	-1.7	ns
solyc09g050020.1.1	6	Uncharacterized protein	PS.lightreaction.cytochrome b6/f.cytochrome b6 (CYB6)	-10	4.3E-02	0.9	ns	0.7	ns	1.4	ns
solyc03g117850.2.1	6	Uncharacterized protein	PS.calvin cycle.rubisco interacting	-7.3	2.3E-05	-3.9	1.4E-02	-1.2	ns	-0.3	ns
solyc05g056270.2.1	6	Uncharacterized protein	gluconeogenese/ glyoxylate cycle.isocitrate lyase	-10	3.3E-04	-3	8.6E-03	-0.5	ns	-0.4	ns
solyc06g073740.2.1	6	Uncharacterized protein	cell wall.degradation.cellulases and beta -1,4-glucanases	-5.6	1.6E-03	0.7	ns	1.1	ns	1	ns
solyc06g068670.2.1	6	Uncharacterized protein	amino acid metabolism	-12.3	5.0E-02	-4	5.0E-02	-0.5	ns	1.5	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc04g050930.2.1	6	Uncharacterized protein	secondary metabolism.isoprenoids.carotenoids.violaxanthin de-epoxidase	-10	3.7E-04	-3.2	9.2E-03	-0.5	ns	0	ns
solyc10g085050.1.1	6	Uncharacterized protein	hormone metabolism.auxin.induced-regulated-responsive-activated	-10	4.6E-04	-1.9	ns	0.5	ns	1.6	ns
solyc05g053340.2.1	6	Gibberellin 2-oxidase	hormone metabolism.ethylene.synthesis-degradation	-9.2	2.5E-02	-1.9	ns	-1.3	ns	0.2	ns
solyc05g053340.2.1	6	Gibberellin 2-oxidase	hormone metabolism.gibberelin.synthesis-degradation.GA2 oxidase	-9.2	2.5E-02	-1.9	ns	-1.3	ns	0.2	ns
solyc00g323130.2.1	6	Uncharacterized protein	stress.abiotic.unspecified	-10	5.9E-04	-1.5	ns	-1.6	ns	-0.8	ns
solyc01g087520.2.1	6	Uncharacterized protein	redox.thioredoxin	-9.3	1.9E-02	-1.5	ns	-0.5	ns	0.4	ns
solyc07g043160.1.1	6	Uncharacterized protein	misc.UDP glucosyl and glucoronyl transferases	-10	3.7E-04	-2.5	ns	-0.2	ns	-0.8	ns
solyc03g119080.2.1	6	Uncharacterized protein	misc.gluco-, galacto- and mannosidases	-8	2.9E-04	-0.6	ns	-0.3	ns	0	ns
solyc07g056440.2.1	6	Uncharacterized protein	misc.glutathione S transferases	-10	2.7E-04	-3.9	6.8E-03	-0.2	ns	-0.1	ns
solyc02g081430.2.1	6	Uncharacterized protein	misc.glutathione S transferases	-5.6	ns	-0.2	ns	2.7	3.4E-02	0.1	ns
solyc08g074480.1.1	6	Uncharacterized protein	misc.protease inhibitor/seed storage/lipid transfer protein (LTP) family protein	-10	2.2E-04	-3	5.0E-02	-1.1	ns	-1	ns
solyc12g009650.1.1	6	Putative proline-rich protein (Fragment)	misc.protease inhibitor/seed storage/lipid transfer protein (LTP) family protein	-10	4.0E-04	-3.9	9.9E-03	-1.5	ns	-1.3	ns
solyc01g103100.2.1	6	Uncharacterized protein	misc.short chain dehydrogenase/reductase (SDR)	-10	5.1E-02	-2.3	5.1E-02	-0.7	ns	1.2	ns
solyc06g053140.2.1	6	Uncharacterized protein	misc.rhodanese	-9.4	1.8E-04	-4.9	4.1E-02	-1.8	ns	-0.2	ns
solyc12g017460.1.1	6	Uncharacterized protein	misc.GDSL-motif lipase	-5.2	ns	1.6	5.0E-02	1.5	ns	0.5	ns
solyc08g029120.1.1	6	Uncharacterized protein	RNA.regulation of transcription.Chromatin Remodeling Factors	-10	7.1E-04	-1.3	ns	-0.6	ns	-0.3	ns
solyc10g047930.1.1	6	Uncharacterized protein	RNA.regulation of transcription.putative transcription regulator	-6.2	3.9E-02	-0.3	ns	-0.2	ns	-1.3	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc00g105750.1.1	6	Uncharacterized protein	RNA.regulation of transcription.unclassified	-8.2	5.0E-02	-2.3	5.0E-02	-1.7	ns	-0.1	ns
solyc09g015800.1.1	6	Uncharacterized protein	DNA.unspecified	-10	1.5E-03	1	ns	2	ns	1.4	4.2E-03
solyc09g015310.1.1	6	Uncharacterized protein	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.30S subunit.S4	-10	4.7E-02	-4.1	5.0E-02	-0.8	ns	0.2	ns
solyc11g066410.1.1	6	Uncharacterized protein	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.50S subunit.L9	-10	5.0E-02	-1	ns	-0.3	ns	1.3	ns
solyc06g007570.2.1	6	40S ribosomal protein S8	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S8	-6.9	2.0E-02	-0.6	ns	1.6	ns	1	ns
solyc09g057650.2.1	6	40S ribosomal protein S8	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S8	-4.8	5.0E-02	0.1	ns	2.6	2.2E-02	1.9	ns
solyc07g065170.2.1	6	40S ribosomal protein S8	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S8	-6.1	3.0E-02	-0.1	ns	1.7	ns	1.3	ns
solyc01g099670.2.1	6	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S10	-7.6	6.2E-06	0.2	ns	1.2	ns	0.9	ns
solyc10g078630.1.1	6	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S28	-10	6.9E-04	-3	1.6E-02	1.5	ns	0.4	ns
solyc05g054070.2.1	6	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L6	-6.1	2.0E-03	-0.7	ns	0.1	ns	0	ns
solyc02g068130.2.1	6	Uncharacterized protein	protein.targeting.mitochondria	-5.5	2.7E-02	-0.4	ns	1.3	ns	0.6	ns
solyc01g091580.2.1	6	Uncharacterized protein	protein.targeting.chloroplast	-8.6	1.4E-02	-2.7	ns	-0.3	ns	0.1	ns
solyc06g076360.2.1	6	Uncharacterized protein	protein.targeting.chloroplast	-7.1	1.0E-06	-1.8	ns	-0.2	ns	0.3	ns
solyc04g072630.2.1	6	Uncharacterized protein	protein.targeting.secretory pathway.unspecified	-10	2.6E-04	-2.8	ns	-0.8	ns	-0.1	ns
solyc01g100860.2.1	6	Uncharacterized protein	protein.targeting.secretory pathway.unspecified	-6.9	2.8E-04	-3	1.6E-02	0.4	ns	0.3	ns
solyc03g007110.2.1	6	Uncharacterized protein	protein.targeting.unknown	-10	2.1E-04	-4.5	5.0E-03	-1.6	ns	0.2	ns
solyc02g081550.2.1	6	FtsH protease	protein.degradation.metalloprotease	-6.1	3.3E-02	-1.2	ns	-0.1	ns	0.3	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc01g111640.2.1	6	Uncharacterized protein	protein.degradation.ubiquitin.E3.SCF.SKP	-10	2.8E-04	-3.3	5.2E-02	1.8	ns	0.4	ns
solyc04g080590.2.1	6	Proteasome subunit alpha type	protein.degradation.ubiquitin.proteasom	-5.8	ns	0.1	ns	0.8	ns	0.8	ns
solyc04g012040.2.1	6	Uncharacterized protein	protein.degradation.ubiquitin.proteasom	-10	4.6E-04	-1.9	ns	0.5	ns	1.6	ns
solyc05g013030.1.1	6	Uncharacterized protein	protein.degradation.ubiquitin.proteasom	-10	0.0E+00	-1.1	5.1E-02	0.2	ns	0.1	ns
solyc09g008650.2.1	6	Peptidyl-prolyl cis-trans isomerase	protein.folding	-10	5.0E-02	1.5	5.0E-02	0.7	ns	1.8	ns
solyc01g068400.2.1	6	Uncharacterized protein	protein.folding	-10	4.2E-04	-1.6	ns	-1	ns	-0.5	ns
solyc06g074890.1.1	6	Uncharacterized protein	protein.folding	-10	7.3E-04	-1.4	2.1E-02	-0.2	ns	0.9	ns
solyc01g088610.2.1	6	Uncharacterized protein	protein.folding	-7.4	8.3E-03	-0.7	ns	-0.1	ns	0.3	ns
solyc05g056390.2.1	6	Uncharacterized protein	protein.folding	-10	5.0E-02	1.9	ns	2.2	ns	2.4	ns
solyc01g109410.2.1	6	Dolichyl-diphosphooligosaccharide--protein glycosyltransferase 48 kDa subunit	protein.glycosylation	-10	5.0E-02	3.4	5.0E-02	3.2	ns	2.7	ns
solyc02g080070.2.1	6	Uncharacterized protein	signalling.receptor kinases.DUF 26	-10	ns	1	ns	2.2	ns	1.6	ns
solyc04g048900.2.1	6	Uncharacterized protein	signalling.calcium	-10	ns	2.6	1.5E-03	4.9	1.0E-02	2.8	4.9E-03
solyc10g005100.2.1	6	Uncharacterized protein	signalling.phosphinositides	-10	1.5E-02	-1.5	5.0E-02	-1.2	5.1E-02	0.1	ns
solyc01g109520.2.1	6	Uncharacterized protein	signalling.G-proteins	-10	2.0E-02	-1.5	ns	0.7	ns	0.2	ns
solyc01g079540.2.1	6	Uncharacterized protein	signalling.G-proteins	-5.5	2.7E-02	-0.4	ns	1.3	ns	0.6	ns
solyc03g059420.2.1	6	Uncharacterized protein	development.unspecified	-10	5.0E-02	-1.5	ns	0.3	ns	-0.4	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc10g081530.1.1	6	Uncharacterized protein	transport.p- and v-ATPases.H+-transporting two-sector ATPase	-10	5.0E-02	-0.4	ns	2.6	ns	1.7	ns
solyc11g017010.1.1	6	Sucrose transporter 1	transport.sugars.sucrose	-10	2.3E-05	-7.4	9.6E-03	0.1	ns	-0.6	ns
solyc09g005620.2.1	6	SlGRX1 protein	transport.calcium	-13.4	1.1E-05	-3.9	ns	-0.4	ns	0.6	ns
solyc07g047980.1.1	6	Uncharacterized protein	not assigned.unknown	-8.5	6.1E-04	-2	5.1E-02	-0.4	ns	0.4	ns
solyc10g076350.1.1	6	Uncharacterized protein	not assigned.unknown	-10	3.2E-04	-2.2	ns	0.6	ns	-0.1	ns
solyc11g006060.1.1	6	Uncharacterized protein	not assigned.unknown	-10	9.2E-06	-9	1.3E-04	-1.4	ns	-0.9	ns
solyc09g009510.2.1	6	Uncharacterized protein	not assigned.unknown	-10	6.5E-04	-0.7	ns	0.7	ns	-1	ns
solyc08g082400.1.1	6	Uncharacterized protein	not assigned.unknown	-10	4.5E-04	-1.9	ns	-0.9	ns	-1	ns
solyc01g080260.2.1	6	Uncharacterized protein	not assigned.unknown	-10	5.0E-04	-4.2	5.0E-03	-1.6	ns	-1.1	ns
solyc03g113240.2.1	6	Uncharacterized protein	not assigned.unknown	-10	2.4E-02	-1.2	ns	1.9	ns	-0.4	ns
solyc09g084480.2.1	6	Uncharacterized protein	not assigned.unknown	-5.6	8.5E-03	3.8	ns	-2.1	ns	2.1	ns
solyc10g006370.2.1	6	Uncharacterized protein	not assigned.unknown	-10	1.6E-04	-2.7	5.0E-02	-0.5	ns	-0.2	ns
solyc01g049890.2.1	6	Uncharacterized protein	not assigned.unknown	-6.5	2.8E-02	-1	ns	0.9	ns	0.4	ns
solyc03g065160.1.1	6	Uncharacterized protein	not assigned.unknown	-7.6	ns	-2.7	ns	-1.2	ns	0.1	ns
solyc06g076790.1.1	6	Uncharacterized protein	not assigned.unknown	-11.6	4.1E-05	-2.9	5.1E-02	-1	ns	-0.1	ns
solyc01g079470.2.1	6	Uncharacterized protein	not assigned.unknown	-11.1	4.6E-02	-3	3.8E-02	-0.6	ns	-0.1	ns
solyc04g082200.2.1	6	Uncharacterized protein	not assigned.unknown	-6.8	3.6E-03	1.7	ns	1	ns	1.1	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc07g014700.2.1	6	Uncharacterized protein	not assigned.unknown	-10	ns	2.2	ns	2.7	ns	2.8	5.4E-02
solyc00g006800.2.1	7	Transaldolase	OPP.non-reductive PP.transaldolase	8.1	1.2E-02	7.1	1.8E-02	5.6	2.0E-02	4.2	ns
solyc07g064800.2.1	7	Uncharacterized protein	TCA / org. transformation.TCA.2-oxoglutarate dehydrogenase	10	9.8E-03	10	7.7E-03	10	3.9E-02	10	ns
solyc06g067920.2.1	7	Uncharacterized protein	mitochondrial electron transport / ATP synthesis.cytochrome c	10	8.2E-03	10	1.2E-02	10	ns	10	ns
solyc07g026770.2.1	7	Uncharacterized protein	mitochondrial electron transport / ATP synthesis.F1-ATPase	10	1.1E-02	10	ns	10	ns	10	ns
solyc04g005340.2.1	7	Uncharacterized protein	cell wall.cell wall proteins.RGP	6.6	3.9E-02	5.4	ns	5.1	ns	2.4	ns
solyc08g005800.2.1	7	Uncharacterized protein	cell wall.pectin*esterases.acetyl esterase	8.3	5.2E-04	7.9	5.4E-04	4.9	2.1E-03	3.4	3.4E-03
solyc02g070790.2.1	7	Uncharacterized protein	lipid metabolism.FA synthesis and FA elongation.ketoacyl ACP synthase	10	ns	10	ns	10	5.1E-02	10	5.1E-02
solyc06g068090.2.1	7	Phospholipase D	lipid metabolism.lipid degradation.lysophospholipases	10	1.9E-02	10	ns	10	4.7E-03	10	3.6E-02
solyc12g096190.1.1	7	Uncharacterized protein	amino acid metabolism.synthesis.aromatic aa.tryptophan.tryptophan synthase	7.3	8.0E-03	6	1.5E-02	4.7	2.4E-02	2.5	ns
solyc08g080590.2.1	7	Uncharacterized protein	stress.biotic	7.4	4.6E-02	4.8	5.1E-02	5.6	ns	3.4	ns
solyc07g009510.1.1	7	Uncharacterized protein	stress.biotic	9.8	2.4E-06	8.4	2.8E-05	4.9	5.9E-03	0.1	ns
solyc10g055200.1.1	7	Uncharacterized protein	stress.biotic.PR-proteins	7.1	5.0E-02	6	5.1E-02	5.9	ns	0.7	ns
solyc03g098730.1.1	7	Uncharacterized protein	stress.biotic.PR-proteins.proteinase inhibitors.trypsin inhibitor	10	5.1E-02	10	1.5E-02	10	ns	10	ns
solyc03g111200.2.1	7	Uncharacterized protein	nucleotide metabolism.phosphotransfer and pyrophosphatases.adenylate kinase	9.1	7.9E-04	8.1	1.7E-03	8.1	1.2E-03	5.7	6.4E-03
solyc10g055240.1.1	7	Uncharacterized protein	misc.gluco-, galacto- and mannosidases	6.7	2.9E-02	9.3	1.1E-02	7.1	ns	2.9	ns
solyc03g122350.2.1	7	Uncharacterized protein	misc.cytochrome P450	10	ns	10	ns	10	1.8E-02	10	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc02g079510.2.1	7	Suberization-associated anionic peroxidase 2	misc.peroxidases	9.8	4.7E-02	6.8	1.2E-02	6.6	4.4E-04	0.3	ns
solyc09g092080.2.1	7	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L7/L30/S12	10	3.9E-02	10	4.7E-02	10	ns	10	ns
solyc10g081030.1.1	7	Uncharacterized protein	protein.synthesis.elongation	2.6	ns	10	1.0E-02	9.8	2.0E-02	6.6	ns
solyc06g068960.1.1	7	Uncharacterized protein	signalling.calcium	10	5.3E-03	10	5.0E-02	10	5.7E-03	10	5.1E-02
solyc01g097520.2.1	7	Uncharacterized protein	cell.organisation	7.4	4.4E-02	10.1	2.5E-03	9.1	4.8E-03	7.7	1.3E-02
solyc01g104030.2.1	7	Uncharacterized protein	transport.potassium	10	1.5E-02	10	ns	10	1.3E-02	10	ns
solyc01g095050.2.1	7	Uncharacterized protein	not assigned.unknown	10	ns	10	2.1E-02	10	6.3E-03	10	ns
solyc10g006230.2.1	8	Chlorophyll a-b binding protein 7, chloroplastic	PS.lightreaction.photosystem II.LHC-II	-3.5	1.3E-02	-2.2	ns	-0.3	ns	-0.7	ns
solyc07g063600.2.1	8	Uncharacterized protein	PS.lightreaction.photosystem II.LHC-II	-3	6.1E-05	-1.1	ns	-0.5	ns	-0.3	ns
solyc03g005780.1.1	8	Chlorophyll a-b binding protein 3C, chloroplastic	PS.lightreaction.photosystem II.LHC-II	-1.2	2.1E-02	-0.3	ns	-0.1	ns	-0.1	ns
solyc06g063370.2.1	8	Uncharacterized protein	PS.lightreaction.photosystem II.LHC-II	-2.1	6.9E-05	-1.2	3.4E-02	-0.4	ns	0	ns
solyc01g007520.2.1	8	Photosystem II reaction center protein H	PS.lightreaction.photosystem II.PSII polypeptide subunits	-2.2	2.9E-02	-1.4	5.0E-02	-0.6	ns	-0.5	ns
solyc07g044860.2.1	8	Oxygen-evolving enhancer protein 2, chloroplastic	PS.lightreaction.photosystem II.PSII polypeptide subunits	-2.4	2.1E-04	-0.9	5.0E-02	-0.3	ns	0	ns
solyc09g064500.2.1	8	Photosystem II reaction center Psb28 protein	PS.lightreaction.photosystem II.PSII polypeptide subunits	-2.3	1.4E-02	-1.5	5.0E-02	-0.5	ns	0	ns
solyc09g055950.1.1	8	Photosystem II D2 protein	PS.lightreaction.photosystem II.PSII polypeptide subunits	-1.7	5.4E-03	-0.8	ns	-0.3	ns	0	ns
solyc06g060340.2.1	8	Photosystem II 22 kDa protein, chloroplastic	PS.lightreaction.photosystem II.PSII polypeptide subunits	-3.9	7.4E-05	-2.1	5.0E-02	-0.4	ns	-0.1	ns
solyc01g007500.2.1	8	Photosystem II CP47 reaction center protein	PS.lightreaction.photosystem II.PSII polypeptide subunits	-2.2	9.8E-04	-1	5.0E-02	-0.4	ns	-0.5	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc06g082940.2.1	8	Uncharacterized protein	PS.lightreaction.photosystem I.PSI polypeptide subunits	-3.9	1.6E-03	-2.7	3.9E-02	-0.9	ns	-0.3	ns
solyc07g066150.1.1	8	Uncharacterized protein	PS.lightreaction.photosystem I.PSI polypeptide subunits	-6.1	2.7E-03	-3.6	ns	-1.1	ns	-0.9	ns
solyc06g074200.2.1	8	Uncharacterized protein	PS.lightreaction.photosystem I.PSI polypeptide subunits	-4.1	1.1E-03	-1.8	ns	-0.5	ns	0.2	ns
solyc06g083680.2.1	8	Uncharacterized protein	PS.lightreaction.photosystem I.PSI polypeptide subunits	-1.8	3.2E-03	-0.9	ns	-0.4	ns	0.1	ns
solyc02g069460.2.1	8	Uncharacterized protein	PS.lightreaction.photosystem I.PSI polypeptide subunits	-2.8	4.8E-06	-1.1	ns	-0.4	ns	-0.1	ns
solyc12g005630.1.1	8	Cytochrome b6-f complex iron-sulfur subunit	PS.lightreaction.cytochrome b6/f.iron sulfur subunit	-4.6	4.2E-05	-2.1	ns	-1	ns	-0.4	ns
solyc01g007530.2.1	8	Cytochrome b6	PS.lightreaction.cytochrome b6/f.cytochrome b6 (CYB6)	-6.7	6.2E-06	-3.3	4.3E-03	-0.7	ns	0	ns
solyc01g007380.1.1	8	Apocytochrome f	PS.lightreaction.cytochrome b6/f.apocytochrome f (CYF)	-1.9	2.4E-03	-1.1	5.0E-02	-0.5	ns	-0.2	ns
solyc10g045220.1.1	8	Uncharacterized protein	PS.lightreaction.cytochrome b6/f.apocytochrome f (CYF)	-1.9	4.3E-03	-1	ns	-0.5	ns	-0.2	ns
solyc12g056830.1.1	8	Uncharacterized protein	PS.lightreaction.ATP synthase.delta chain	-3.3	6.4E-05	-1.9	5.0E-02	-0.7	5.3E-03	-0.3	ns
solyc10g044520.1.1	8	Ferredoxin-1, chloroplastic	PS.lightreaction.other electron carrier (ox/red).ferredoxin	-2.9	1.0E-05	-1.3	5.1E-02	-0.6	ns	-0.2	ns
solyc11g006020.1.1	8	Uncharacterized protein	PS.lightreaction.NADH DH	-3.2	8.6E-03	-1	ns	-1.1	ns	-0.5	ns
solyc10g047460.1.1	8	Uncharacterized protein	PS.lightreaction.cyclic electron flow-chlororespiration	-5.1	5.0E-02	-3.5	5.1E-02	-1	ns	-0.1	ns
solyc09g090570.2.1	8	Uncharacterized protein	PS.lightreaction.cyclic electron flow-chlororespiration	-4	1.6E-02	-2	ns	-1.2	ns	-0.3	ns
solyc06g061070.2.1	8	Uncharacterized protein	PS.photorespiration.glycine cleavage.H protein	-2.2	3.6E-04	-1.1	5.0E-02	-0.5	ns	-0.4	ns
solyc08g007040.2.1	8	Uncharacterized protein	PS.photorespiration.glycine cleavage.H protein	-2.7	1.6E-04	-1.7	2.7E-02	-0.7	ns	-0.4	ns
solyc03g120430.2.1	8	Uncharacterized protein	PS.photorespiration.glycerate kinase	-4.1	8.7E-04	-1.2	5.0E-02	-0.8	ns	0.1	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc06g009630.1.1	8	Uncharacterized protein	PS.calvin cycle	-2.2	1.4E-03	-1.2	5.0E-02	-0.2	ns	0.1	ns
solyc02g077860.1.1	8	Uncharacterized protein	PS.calvin cycle.rubisco large subunit	-4.3	3.0E-04	-2.2	5.0E-02	-1	ns	-0.5	ns
solyc04g011510.2.1	8	Triosephosphate isomerase	PS.calvin cycle.TPI	-2	6.2E-06	-1.3	1.8E-03	-0.5	ns	-0.2	ns
solyc06g005490.2.1	8	Triosephosphate isomerase	PS.calvin cycle.TPI	-2.1	4.1E-05	-1.2	3.2E-02	-0.4	ns	-0.3	ns
solyc07g056140.2.1	8	Glucose-1-phosphate adenylyltransferase	major CHO metabolism.synthesis.starch.AGPase	-2	5.6E-04	-1	ns	-0.1	ns	0	ns
solyc10g007050.2.1	8	Uncharacterized protein	minor CHO metabolism.others	-5.1	4.1E-02	-3.9	4.9E-02	-1.8	ns	-0.4	ns
solyc04g011510.2.1	8	Triosephosphate isomerase	glycolysis.cytosolic branch.triosephosphate isomerase (TPI)	-2	6.2E-06	-1.3	1.8E-03	-0.5	ns	-0.2	ns
solyc06g005490.2.1	8	Triosephosphate isomerase	glycolysis.cytosolic branch.triosephosphate isomerase (TPI)	-2.1	4.1E-05	-1.2	3.2E-02	-0.4	ns	-0.3	ns
solyc04g076090.2.1	8	Glucose-6-phosphate isomerase	glycolysis.plastid branch.glucose-6-phosphate isomerase	-1.1	ns	0	ns	0.9	ns	1.3	ns
solyc04g076090.2.1	8	Glucose-6-phosphate isomerase	glycolysis.unclear/dually targeted.glucose-6-phosphate isomerase	-1.1	ns	0	ns	0.9	ns	1.3	ns
solyc09g090900.2.1	8	Uncharacterized protein	TCA / org. transformation.TCA.aconitase	-4.2	4.8E-02	-0.1	ns	0.9	ns	1.5	ns
solyc11g056410.1.1	8	Uncharacterized protein	mitochondrial electron transport / ATP synthesis.cytochrome c oxidase	-1.4	3.1E-02	-0.3	ns	0.2	ns	0.3	ns
solyc03g115110.2.1	8	Uncharacterized protein	mitochondrial electron transport / ATP synthesis.F1-ATPase	-2.7	1.4E-03	-0.2	ns	0	ns	0.3	ns
solyc06g005020.1.1	8	Uncharacterized protein	mitochondrial electron transport / ATP synthesis.F1-ATPase	-1.9	1.8E-02	0.3	ns	0.1	ns	-0.3	ns
solyc02g067080.2.1	8	UDP-glucose 6-dehydrogenase	cell wall.precursor synthesis.UGD	-3.4	5.1E-02	-1.2	ns	0.2	ns	0.4	ns
solyc07g065360.1.1	8	Uncharacterized protein	cell wall.pectin*esterases.PME	-6.4	2.9E-02	-2.5	5.0E-02	-0.7	ns	-0.2	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc01g008330.2.1	8	Uncharacterized protein	lipid metabolism.FA synthesis and FA elongation.Acetyl CoA Carboxylation.heteromeric Complex.Biotin Carboxylase	-3.5	5.1E-02	-0.2	ns	0.3	ns	-0.1	ns
solyc01g105060.2.1	8	Uncharacterized protein	lipid metabolism.FA synthesis and FA elongation.beta hydroxyacyl ACP dehydratase	-4.1	4.4E-06	-0.6	ns	0.4	ns	0	ns
solyc03g117890.2.1	8	Uncharacterized protein	amino acid metabolism	-4.4	4.1E-06	-1.7	2.1E-02	-0.7	ns	-0.1	ns
solyc10g081510.1.1	8	Uncharacterized protein	amino acid metabolism.synthesis.aspartate family.methionine	-3.6	6.7E-03	-0.5	ns	0.9	ns	0.6	ns
solyc11g044840.1.1	8	Uncharacterized protein	amino acid metabolism.synthesis.aromatic aa.phenylalanine and tyrosine	-3.6	9.8E-06	-2.2	2.6E-03	-1.1	5.6E-02	-0.4	ns
solyc01g102820.2.1	8	Uncharacterized protein	secondary metabolism.isoprenoids.non-mevalonate pathway.CMS	-1.1	1.1E-02	-0.3	ns	0.2	ns	0	ns
solyc11g069380.1.1	8	GcpE	secondary metabolism.isoprenoids.non-mevalonate pathway.HDS	-3.1	6.1E-03	-1.8	ns	-0.2	ns	-0.1	ns
solyc05g014330.1.1	8	Uncharacterized protein	secondary metabolism.phenylpropanoids	-5.4	2.2E-04	-2.8	1.0E-02	-0.6	ns	-0.5	ns
solyc07g049660.2.1	8	Uncharacterized protein	secondary metabolism.phenylpropanoids	-3.8	ns	0.6	ns	3.6	5.3E-02	1.6	ns
solyc01g079200.2.1	8	Gibberellin 2-oxidase	hormone metabolism.ethylene.synthesis-degradation	-1.5	8.7E-04	0.1	ns	0.6	6.4E-02	-0.1	ns
solyc01g111080.2.1	8	Snakin-2	hormone metabolism.gibberelin.induced-regulated-responsive-activated	-4.7	1.5E-02	-1.6	ns	-0.8	ns	1.4	ns
solyc01g006560.2.1	8	Lipoxygenase	hormone metabolism.jasmonate.synthesis-degradation.lipoxygenase	-3.3	8.9E-05	-1.3	ns	-1.1	ns	0	ns
solyc01g009680.2.1	8	Lipoxygenase	hormone metabolism.jasmonate.synthesis-degradation.lipoxygenase	-6.4	7.8E-03	-1.3	ns	-1.2	ns	0.1	ns
solyc07g049690.2.1	8	Uncharacterized protein	hormone metabolism.jasmonate.synthesis-degradation.allene oxidase synthase	-3.9	8.7E-05	-1	ns	0	ns	0.4	ns
solyc07g054210.2.1	8	Uncharacterized protein	tetrapyrrole synthesis.protochlorophyllide reductase	-3	1.3E-03	-1.8	ns	0.1	ns	0.4	ns
solyc12g005180.1.1	8	Uncharacterized protein	stress.abiotic	-3.5	7.9E-03	0.2	ns	0.2	ns	0.3	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc04g007790.2.1	8	Uncharacterized protein	stress.abiotic.unspecified	-5.2	1.5E-06	-2.6	1.1E-03	-1.7	9.1E-03	-0.5	ns
solyc05g056300.2.1	8	Uncharacterized protein	redox.thioredoxin	-3.9	5.0E-02	-1.6	5.1E-02	-0.1	ns	0.1	ns
solyc06g005940.2.1	8	Protein disulfide-isomerase	redox.thioredoxin	-1	ns	-0.1	ns	0.6	ns	0.2	ns
solyc02g085520.2.1	8	Adenylosuccinate synthetase, chloroplastic	nucleotide metabolism.synthesis.purine.adenylosuccinate synthase	-4	5.1E-02	-1	ns	0.7	ns	2	ns
solyc08g082430.2.1	8	Nucleoside diphosphate kinase	nucleotide metabolism.phosphotransfer and pyrophosphatases.nucleoside diphosphate kinase	-3.6	2.7E-03	-2.3	2.9E-02	-0.3	ns	-0.1	ns
solyc03g110960.2.1	8	Nucleoside diphosphate kinase	nucleotide metabolism.phosphotransfer and pyrophosphatases.nucleoside diphosphate kinase	-1.7	9.8E-04	-0.3	ns	0.1	ns	0.3	ns
solyc01g060020.2.1	8	Glucan endo-1,3-beta-glucosidase B	misc.beta 1,3 glucan hydrolases.glucan endo-1,3-beta-glucosidase	-2.3	7.8E-05	-0.5	ns	-0.9	1.2E-02	-0.5	ns
solyc09g059040.2.1	8	Uncharacterized protein	misc.oxidases - copper, flavone etc.	-4.9	5.0E-02	-1	ns	0.4	ns	0.9	ns
solyc10g009570.2.1	8	Uncharacterized protein	misc.rhodanese	-4	2.0E-02	-2.1	ns	-2.1	3.9E-02	-0.2	ns
solyc03g059180.2.1	8	Uncharacterized protein	misc.rhodanese	-2.9	3.6E-04	-1.2	5.1E-02	-0.3	ns	0.1	ns
solyc11g008990.1.1	8	Uncharacterized protein	RNA.regulation of transcription.unclassified	-3.4	1.2E-03	-1.1	ns	-0.3	ns	0.1	ns
solyc09g007850.2.1	8	Uncharacterized protein	RNA.RNA binding	-2.2	2.9E-03	-0.5	ns	-0.5	ns	0.1	ns
solyc10g051390.1.1	8	Glycine rich RNA binding protein 1a	RNA.RNA binding	-3.6	2.8E-03	-1.8	5.1E-02	-0.2	ns	-0.2	ns
solyc07g005320.2.1	8	Uncharacterized protein	RNA.RNA binding	-5.4	2.1E-04	-1	ns	-0.3	ns	0.3	ns
solyc11g072840.1.1	8	Histone H4	DNA.synthesis/chromatin structure.histone	-1.9	2.8E-05	-0.2	ns	0.5	ns	0.2	ns
solyc08g074290.2.1	8	Uncharacterized protein	DNA.repair	-2.7	3.2E-04	-0.6	ns	0	ns	0.2	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc01g007280.2.1	8	30S ribosomal protein S4, chloroplastic	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.30S subunit.S4	-6.4	4.4E-02	-2.5	2.0E-02	-0.7	ns	-0.2	ns
solyc09g007560.2.1	8	Uncharacterized protein	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.50S subunit.L5	-2.6	2.7E-02	-1	ns	0.1	ns	0.4	ns
solyc02g086730.1.1	8	Uncharacterized protein	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.50S subunit.L12	-2.8	2.0E-04	-1.4	5.0E-02	-0.4	ns	0.1	ns
solyc12g098890.1.1	8	Uncharacterized protein	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.50S subunit.L18	-3.8	1.8E-02	-1.9	5.0E-02	-1.8	ns	-0.4	ns
solyc08g078010.2.1	8	Uncharacterized protein	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.50S subunit.L19	-2.6	9.4E-05	-1.9	3.3E-03	-0.4	ns	-0.1	ns
solyc07g063960.2.1	8	Uncharacterized protein	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.50S subunit.L24	-4.1	3.7E-05	-1.1	ns	0.2	ns	0.4	ns
solyc08g061850.2.1	8	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S3	-0.8	ns	0	ns	1	9.5E-03	0.6	ns
solyc10g006070.2.1	8	40S ribosomal protein S8	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S8	-4.2	5.5E-03	-0.6	ns	1.5	ns	0.9	ns
solyc06g084230.2.1	8	40S ribosomal protein S24	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S24	-2.6	1.2E-02	-1.6	4.8E-02	0.5	ns	0.3	ns
solyc11g012110.1.1	8	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L6	-3	1.1E-03	-0.2	ns	0.2	ns	-0.3	ns
solyc07g063890.2.1	8	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L8	-1.5	5.1E-02	0.2	ns	0.6	ns	-0.1	ns
solyc12g005330.1.1	8	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L8	-1.4	8.1E-02	0.1	ns	0.5	ns	0.3	ns
solyc03g121330.2.1	8	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L28	-3.5	4.8E-02	1	ns	1.1	ns	0.6	ns
solyc01g094560.2.1	8	60S ribosomal protein L36	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L36	-2.2	5.1E-02	-2	5.1E-02	1.6	ns	1.7	ns
solyc01g097760.2.1	8	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L7A	-5.3	3.9E-02	-2.4	5.1E-02	0.4	ns	-0.6	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc06g064470.2.1	8	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L7A	-2.5	5.2E-03	-0.8	ns	0.4	ns	-0.4	ns
solyc05g054580.2.1	8	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.P0	-1.6	ns	0.2	ns	0.8	ns	0.6	ns
solyc11g028100.1.1	8	Uncharacterized protein	protein.synthesis.elongation	-2.1	6.6E-04	-0.5	ns	0.3	ns	-0.2	ns
solyc06g011280.2.1	8	Uncharacterized protein	protein.synthesis.elongation	-1.4	ns	-0.6	ns	0.7	ns	-0.1	ns
solyc08g079180.2.1	8	Uncharacterized protein	protein.synthesis.elongation	-3.9	2.5E-04	-2.2	4.0E-02	-1.2	ns	0.1	ns
solyc01g095550.2.1	8	Uncharacterized protein	protein.postranslational modification	-4.2	1.4E-05	-1.4	ns	0.1	ns	0.3	ns
solyc06g034020.2.1	8	Methionine sulfoxide reductase A3	protein.postranslational modification	-1.1	ns	0.1	ns	0.2	ns	0.3	ns
solyc01g097770.2.1	8	Phototropin-2	protein.postranslational modification	-2.1	1.4E-02	-0.8	ns	0.1	ns	0.4	ns
solyc03g093690.2.1	8	Methionine sulfoxide reductase A4	protein.postranslational modification	-1.3	7.5E-03	-0.3	ns	-0.1	ns	0	ns
solyc08g068230.2.1	8	Uncharacterized protein	protein.postranslational modification	-2.2	3.9E-05	-1.1	ns	-0.6	ns	-0.1	ns
solyc08g076990.2.1	8	Uncharacterized protein	protein.degradation	-4.8	4.8E-02	0.4	ns	-2.8	ns	1	ns
solyc08g076970.2.1	8	Uncharacterized protein	protein.degradation	-5.8	5.2E-03	-0.1	ns	-2.9	ns	0.9	ns
solyc04g080960.2.1	8	Uncharacterized protein	protein.degradation.cysteine protease	-4.3	1.9E-04	-2	3.6E-02	-0.1	ns	-0.8	ns
solyc01g101240.2.1	8	Aspartic protease	protein.degradation.aspartate protease	-2.7	ns	0.1	ns	1.9	ns	0.3	ns
solyc02g086830.2.1	8	Uncharacterized protein	protein.degradation.serine protease	-1.4	ns	0.3	ns	0.9	ns	0.4	ns
solyc06g083040.2.1	8	Uncharacterized protein	protein.degradation.serine protease	-2.8	1.5E-03	-1.1	ns	-0.5	ns	-0.1	ns
solyc06g083020.1.1	8	Carboxypeptidase	protein.degradation.serine protease	-2.2	1.5E-02	-0.6	ns	-0.6	ns	-0.6	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc08g075750.2.1	8	ATP-dependent Clp protease proteolytic subunit	protein.degradation.serine protease	-0.2	ns	2.8	5.1E-02	3.1	ns	2.3	ns
solyc03g097020.2.1	8	Uncharacterized protein	protein.degradation.AAA type	-5.4	5.8E-04	-1.7	ns	0.5	ns	0.8	ns
solyc08g006540.2.1	8	Peptidyl-prolyl cis-trans isomerase	protein.folding	-2.1	5.3E-02	-0.5	ns	0.1	ns	0.3	ns
solyc02g064940.1.1	8	Uncharacterized protein	signalling.receptor kinases.leucine rich repeat XI	-1.6	1.7E-02	-0.5	ns	-0.3	ns	0.1	ns
solyc04g011360.2.1	8	Uncharacterized protein	signalling.G-proteins	-1.1	ns	-0.3	ns	0.6	ns	0.4	ns
solyc03g079900.2.1	8	Uncharacterized protein	signalling.G-proteins	-4	5.6E-03	-1.4	ns	1.4	ns	0	ns
solyc01g086850.2.1	8	Uncharacterized protein	signalling.G-proteins	-2.6	5.1E-02	-1.3	ns	2.1	8.4E-04	-0.2	ns
solyc10g008840.2.1	8	Uncharacterized protein	signalling.G-proteins	-2.6	ns	-1.3	ns	2.1	8.4E-04	-0.2	ns
solyc09g098170.2.1	8	Uncharacterized protein	signalling.G-proteins	-2.6	ns	-1.3	ns	2.1	8.4E-04	-0.2	ns
solyc03g034180.2.1	8	Uncharacterized protein	signalling.14-3-3 proteins	-1.1	2.9E-02	-0.4	ns	0.3	ns	0	ns
solyc11g010200.1.1	8	14-3-3 protein 6	signalling.14-3-3 proteins	-1.2	1.9E-03	-0.4	ns	0.3	ns	0	ns
solyc04g074510.2.1	8	14-3-3 protein 3	signalling.14-3-3 proteins	-1.3	1.5E-03	-0.6	ns	0.2	ns	0	ns
solyc04g012120.2.1	8	Uncharacterized protein	signalling.14-3-3 proteins	-1	1.2E-02	-0.3	ns	0.3	ns	0	ns
solyc05g054830.2.1	8	Uncharacterized protein	cell.organisation	-3.7	1.5E-03	-0.7	ns	-0.4	ns	-0.1	ns
solyc08g074290.2.1	8	Uncharacterized protein	cell.organisation	-2.7	3.2E-04	-0.6	ns	0	ns	0.2	ns
solyc10g081580.1.1	8	Uncharacterized protein	cell.vesicle transport	-2.5	1.3E-04	-1.6	2.6E-02	-0.3	ns	0.2	ns
solyc08g015690.2.1	8	Uncharacterized protein	development.late embryogenesis abundant	-4.5	2.8E-03	-0.4	ns	1	ns	0.5	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc01g087750.2.1	8	Uncharacterized protein	development.unspecified	-5.6	3.7E-02	-1.9	ns	0	ns	0.2	ns
solyc12g010360.1.1	8	Uncharacterized protein	transport.p- and v-ATPases	-3.6	4.9E-04	-2.8	9.9E-03	-0.3	ns	-0.8	ns
solyc07g005040.2.1	8	Uncharacterized protein	transport.p- and v-ATPases	-5.4	8.0E-04	-3.1	8.9E-03	-0.3	ns	-0.8	ns
solyc07g017780.2.1	8	Uncharacterized protein	transport.p- and v-ATPases	-4.7	3.3E-05	-4	1.3E-03	-0.2	ns	-0.9	ns
solyc08g078200.1.1	8	Uncharacterized protein	transport.p- and v-ATPases	-4.2	9.5E-05	-3.1	5.0E-03	-0.6	ns	-0.7	ns
solyc10g008980.2.1	8	Uncharacterized protein	transport.metabolite transporters at the envelope membrane	-4.8	1.4E-05	-2	4.7E-02	-0.6	ns	-0.1	ns
solyc08g081190.2.1	8	Plasmamembrane intrinsic protein 15	transport.Major Intrinsic Proteins.PIP	-4.8	7.2E-05	-1.3	ns	-0.4	ns	-0.1	ns
solyc11g069430.1.1	8	Uncharacterized protein	transport.Major Intrinsic Proteins.PIP	-4.3	2.2E-04	0.4	ns	0.4	ns	-0.2	ns
solyc09g018750.2.1	8	Uncharacterized protein	not assigned.unknown	-2.3	5.0E-02	-0.4	ns	0.3	ns	1	ns
solyc10g081120.1.1	8	Alpha-L-arabinofuranosidase	not assigned.unknown	-2.5	7.3E-03	1.7	9.5E-03	1	ns	1.2	ns
solyc08g076290.2.1	8	Uncharacterized protein	not assigned.unknown	-3.7	2.5E-05	-2.5	1.6E-03	-0.8	ns	-0.2	ns
solyc01g098640.2.1	8	Uncharacterized protein	not assigned.unknown	-4.9	2.9E-02	-1.7	5.0E-07	-0.6	ns	0.1	ns
solyc03g082890.2.1	8	Uncharacterized protein	not assigned.unknown	-1.9	5.6E-02	-0.6	ns	-0.4	ns	0.3	ns
solyc07g044840.2.1	8	Uncharacterized protein	not assigned.unknown	-4.3	5.0E-04	-1.3	ns	-0.4	ns	-0.1	ns
solyc01g099780.2.1	8	Uncharacterized protein	not assigned.unknown	-2.5	2.1E-06	-0.6	ns	-0.2	ns	-0.1	ns
solyc03g098790.1.1	8	Inhibitor of yeast proteinase A (Fragment)	not assigned.unknown	-1.5	ns	1.7	ns	-1.8	ns	2.3	ns
solyc01g099770.2.1	8	Translationally-controlled tumor protein homolog	not assigned.unknown	-2.8	8.0E-07	-0.7	ns	-0.3	ns	0	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc03g006870.2.1	8	Uncharacterized protein	not assigned.unknown	-3.9	1.4E-03	-1.9	5.0E-02	-0.6	ns	-0.6	ns
solyc08g079240.2.1	8	Uncharacterized protein	not assigned.unknown	-2	2.7E-02	-0.8	ns	-0.5	ns	0.1	ns
solyc12g009600.1.1	8	Uncharacterized protein	not assigned.unknown	-2.8	6.0E-04	-0.7	ns	-0.3	ns	0	ns
solyc10g077080.1.1	8	Uncharacterized protein	not assigned.unknown	-2.5	7.3E-03	1.7	9.5E-03	1	ns	1.2	ns
solyc09g084490.2.1	8	Uncharacterized protein	not assigned.unknown	-6.8	5.1E-02	-1.5	ns	-2.3	ns	1.2	ns
solyc07g054820.2.1	8	Uncharacterized protein	not assigned.unknown	-2.5	1.0E-07	-1.6	3.1E-05	-0.3	ns	0	ns
solyc03g115020.2.1	8	Uncharacterized protein	not assigned.unknown	-1.4	5.1E-02	-0.4	ns	0.1	ns	0.2	ns
solyc01g016980.1.1	8	Uncharacterized protein	not assigned.unknown	-4.1	ns	-1.2	ns	1.3	ns	0.4	ns
solyc01g016680.1.1	8	Uncharacterized protein	not assigned.unknown	-3.5	2.6E-02	-1.2	ns	0.6	ns	0.7	ns
solyc01g100760.2.1	8	Uncharacterized protein	not assigned.unknown	-4.5	ns	-0.1	ns	2.3	ns	2.3	5.0E-02
solyc04g071620.2.1	8	ASR4	not assigned.unknown	-2.3	1.6E-02	0.5	ns	0.5	ns	1.4	4.0E-02
solyc12g019550.1.1	8	Uncharacterized protein	not assigned.unknown	-3.3	3.1E-03	-0.8	ns	-0.3	ns	0.3	ns
solyc11g009020.1.1	8	Uncharacterized protein	not assigned.unknown	-3.2	1.5E-03	-2	1.5E-02	-0.8	ns	0.2	ns
solyc01g095430.2.1	8	Uncharacterized protein	not assigned.unknown	-5.3	2.6E-06	-1.7	5.0E-02	-0.1	ns	0.2	ns
solyc01g096660.2.1	8	Uncharacterized protein	not assigned.unknown	-5	7.0E-07	-2.5	9.4E-04	-0.5	ns	-0.4	ns
solyc10g084730.1.1	8	Uncharacterized protein	not assigned.unknown	-1.8	1.4E-02	1.2	4.9E-02	0.5	ns	1.1	ns
solyc08g067840.2.1	9	Uncharacterized protein	PS.lightreaction.photosystem II.PSII polypeptide subunits	3.6	5.2E-02	2.7	5.3E-02	-1	ns	-1.8	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc01g106010.2.1	9	Uncharacterized protein	PS.calvin cycle.FBPase	3	2.0E-04	-0.1	ns	0.7	ns	-0.2	ns
solyc05g013160.2.1	9	Uncharacterized protein	PS.calvin cycle.rubisco interacting	6.3	3.7E-03	3.3	ns	1	ns	-0.9	ns
solyc10g083290.1.1	9	Cell-wall invertase	major CHO metabolism.degradation.sucrose.invertases.cell wall	5.2	8.4E-03	4.4	5.1E-02	2	ns	-2.2	ns
both	9	Uncharacterized protein	major CHO metabolism.degradation.sucrose.invertases.vacuolar	2.6	1.7E-04	2.1	8.3E-04	3	6.9E-05	0.9	ns
solyc10g005510.2.1	9	Glyceraldehyde-3-phosphate dehydrogenase	glycolysis.cytosolic branch.glyceraldehyde 3-phosphate dehydrogenase (GAP-DH)	2.9	1.8E-04	1.6	1.3E-02	0.8	ns	0.9	ns
solyc12g014380.1.1	9	Glucose-6-phosphate isomerase	glycolysis.plastid branch.glucose-6-phosphate isomerase	4.2	3.7E-03	1.5	ns	-0.6	ns	0	ns
solyc04g008740.2.1	9	Pyruvate kinase	glycolysis.plastid branch.pyruvate kinase (PK)	6.2	5.1E-02	4.6	5.0E-02	2	ns	0.6	ns
solyc12g014380.1.1	9	Glucose-6-phosphate isomerase	glycolysis.unclear/dually targeted.glucose-6-phosphate isomerase	4.2	3.7E-03	1.5	ns	-0.6	ns	0	ns
solyc03g114150.2.1	9	Uncharacterized protein	fermentation.aldehyde dehydrogenase	2.1	5.5E-04	1.6	1.2E-02	0.3	ns	0.4	ns
solyc02g086970.2.1	9	Uncharacterized protein	fermentation.aldehyde dehydrogenase	3.9	8.5E-05	3.1	3.4E-03	0.3	ns	0.3	ns
solyc08g013860.2.1	9	Malic enzyme	TCA / org. transformation.other organic acid transformaitons.malic	2.7	5.1E-02	2.3	5.0E-02	0.9	ns	0.7	ns
solyc01g094200.2.1	9	Malic enzyme	TCA / org. transformation.other organic acid transformaitons.malic	3.8	1.6E-04	3	8.6E-04	2.6	3.5E-03	2.1	1.6E-02
solyc09g064450.2.1	9	Uncharacterized protein	mitochondrial electron transport / ATP synthesis.NADH-DH.localisation not clear	3.3	3.5E-03	1.1	ns	2.4	ns	0.5	ns
solyc04g074550.2.1	9	Uncharacterized protein	mitochondrial electron transport / ATP synthesis.cytochrome c oxidase	2	1.9E-04	2.3	2.7E-05	1.1	ns	-0.5	ns
solyc01g104950.2.1	9	Uncharacterized protein	cell wall.degradation.mannan-xylose-arabinose-fucose	1.3	ns	2.4	1.2E-04	1	ns	0.5	ns
solyc08g006560.2.1	9	Uncharacterized protein	lipid metabolism.FA synthesis and FA elongation.ketoacyl ACP synthase	2.5	9.2E-03	1.2	ns	0.9	ns	0.8	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6hom o/MM fold	T6hom o/MM_ P val	T19ho mo/M M_fold	T19ho mo/MM _P val	T6hem i/MM_ fold	T6hem i/MM_ P val	T19he mi/M M_fold	T19he mi/MM _P val
solyc04g00 8740.2.1	9	Pyruvate kinase	lipid metabolism.FA synthesis and FA elongation.pyruvate kinase	6.2	5.1E-02	4.6	5.0E-02	2	ns	0.6	ns
solyc11g00 7690.1.1	9	Pyruvate kinase	lipid metabolism.FA synthesis and FA elongation.pyruvate kinase	1.9	5.0E-02	2.6	5.0E-02	2	ns	-0.6	ns
solyc10g07 5090.1.1	9	Non-specific lipid-transfer protein	lipid metabolism.lipid transfer proteins etc	1.8	7.5E-02	2.1	2.3E-02	2.5	1.8E-02	2	ns
solyc10g07 5100.1.1	9	Non-specific lipid-transfer protein	lipid metabolism.lipid transfer proteins etc	2.6	1.9E-02	1.7	ns	2.6	1.4E-02	2.7	3.7E-02
solyc10g07 5110.1.1	9	Non-specific lipid-transfer protein 1	lipid metabolism.lipid transfer proteins etc	2.1	1.4E-02	2	1.5E-02	2.5	1.0E-02	1.9	ns
solyc10g00 6650.2.1	9	Uncharacterized protein	lipid metabolism.'exotics' (steroids, squalene etc)	2.2	3.0E-02	1.2	ns	2.5	2.9E-02	0.4	ns
solyc03g12 3610.2.1	9	Uncharacterized protein	amino acid metabolism.synthesis.central amino acid metabolism.alanine.alanine aminotransferase	3.3	7.2E-03	1.2	ns	2	ns	-0.1	ns
solyc05g01 2270.2.1	9	Uncharacterized protein	amino acid metabolism.synthesis.glutamate family.arginine.arginosuccinate synthase	3.4	5.1E-02	3.1	ns	0	ns	-0.5	ns
solyc10g04 9890.1.1	9	Uncharacterized protein	amino acid metabolism.synthesis.serine-glycine-cysteine group.serine.phosphoglycerate dehydrogenase	3.3	5.0E-02	1.9	5.0E-02	1.8	ns	1.2	ns
solyc03g12 3830.2.1	9	Uncharacterized protein	amino acid metabolism.synthesis.serine-glycine-cysteine group.serine.phosphoglycerate dehydrogenase	3.4	5.1E-02	2.4	5.0E-02	2.2	ns	1.3	ns
solyc06g07 1000.2.1	9	Uncharacterized protein	amino acid metabolism.degradation.glutamate family.proline	3.1	7.3E-04	2.4	4.7E-03	2	2.3E-02	1.6	ns
solyc08g06 6850.2.1	9	Lactoylglutathione lyase	amino acid metabolism.degradation.aspartate family.threonine	3.1	2.3E-03	2.4	2.0E-02	-0.1	ns	0.5	ns
solyc06g05 0980.2.1	9	Ferritin	metal handling.binding, chelation and storage	2.5	4.7E-02	1.6	ns	3.7	2.3E-04	1	ns
solyc05g05 2470.2.1	9	Ferritin	metal handling.binding, chelation and storage	3.6	3.5E-03	2.7	ns	4.2	5.6E-04	1.3	ns
solyc02g03 6350.2.1	9	1-aminocyclopropane-1-carboxylate oxidase	hormone metabolism.ethylene.synthesis-degradation	3.1	2.1E-03	1.3	ns	1.4	ns	1.4	ns
solyc02g08 2920.2.1	9	Chitinase	stress.biotic	2.9	4.9E-05	1.6	5.7E-03	2.2	7.7E-04	-0.3	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc05g050130.2.1	9	Uncharacterized protein	stress.biotic	4.9	0.0E+00	4.6	1.0E-07	4.4	1.0E-07	1.7	3.4E-03
solyc07g005100.2.1	9	Uncharacterized protein	stress.biotic	3	5.0E-02	3	2.4E-03	1.4	ns	0.2	ns
solyc01g095250.1.1	9	Uncharacterized protein	stress.biotic	6.1	2.8E-06	5.6	1.3E-05	4.9	2.7E-05	1.6	ns
solyc12g043110.1.1	9	Uncharacterized protein	stress.abiotic.heat	3.1	2.4E-02	2.5	5.0E-02	2.5	ns	-0.7	ns
solyc12g015880.1.1	9	Molecular chaperone Hsp90-1	stress.abiotic.heat	2.5	7.3E-04	2.2	2.2E-03	2.2	5.3E-03	1.2	ns
solyc07g065840.2.1	9	Molecular chaperone Hsp90-2	stress.abiotic.heat	2.6	5.6E-03	2.2	2.1E-03	2.1	5.6E-04	1.1	ns
solyc03g025810.2.1	9	Uncharacterized protein	stress.abiotic.cold	2.4	5.4E-03	1.5	5.1E-02	1.2	ns	0.7	ns
solyc07g063680.2.1	9	Uncharacterized protein	stress.abiotic.unspecified	2.8	9.8E-04	1.1	5.1E-02	0.9	ns	0.2	ns
solyc04g007760.2.1	9	Uncharacterized protein	stress.abiotic.unspecified	5.5	1.1E-03	5.8	2.0E-03	2.3	ns	0.2	ns
solyc03g025950.2.1	9	Uncharacterized protein	redox.ascorbate and glutathione	3.5	9.6E-05	2.5	3.8E-02	2	ns	0.9	ns
solyc09g091840.2.1	9	Uncharacterized protein	redox.ascorbate and glutathione.glutathione	2.8	1.9E-02	1.8	5.0E-02	1	ns	-0.6	ns
solyc06g005260.2.1	9	Uncharacterized protein	redox.glutaredoxins	2.8	3.6E-05	1.9	1.5E-03	1.5	1.6E-02	0.00E+00	ns
solyc01g067740.2.1	9	Superoxide dismutase [Cu-Zn]	redox.dismutases and catalases	3.5	5.1E-02	1.7	5.1E-02	-0.2	ns	0.5	ns
solyc06g049080.2.1	9	Superoxide dismutase	redox.dismutases and catalases	2	1.7E-03	1.4	3.5E-02	0.8	ns	0.3	ns
solyc03g115630.2.1	9	Uncharacterized protein	nucleotide metabolism.synthesis.pyrimidine.carbamoyl phosphate synthetase	5.7	5.0E-02	4.1	5.1E-02	0.5	ns	0.4	ns
solyc02g069800.1.1	9	Uncharacterized protein	Biodegradation of Xenobiotics	4.9	4.8E-02	4.5	5.0E-02	5.5	ns	1.4	ns
solyc02g086880.2.1	9	Formate dehydrogenase	C1-metabolism	4.7	4.6E-06	3.3	1.2E-04	2.9	9.4E-04	1.2	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc04g009630.2.1	9	Uncharacterized protein	misc.gluco-, galacto- and mannosidases.alpha-galactosidase	6.4	2.3E-02	6	2.3E-02	4.6	2.4E-02	0.2	ns
solyc09g011600.2.1	9	Glutathione S-transferase-like protein	misc.glutathione S transferases	3.8	7.7E-03	1.9	5.1E-02	0.9	ns	-0.3	ns
solyc09g011580.2.1	9	Uncharacterized protein	misc.glutathione S transferases	3.8	8.0E-03	1.9	5.0E-02	0.9	ns	-0.3	ns
solyc09g011630.2.1	9	Putative glutathione S-transferase T2	misc.glutathione S transferases	3.6	4.9E-03	1.9	ns	0.7	ns	-0.7	ns
solyc12g056250.1.1	9	Uncharacterized protein	misc.glutathione S transferases	3.1	7.9E-03	2.9	1.0E-02	1.5	ns	0.2	ns
solyc01g006300.2.1	9	Peroxidase	misc.peroxidases	2.9	5.1E-02	2.3	4.7E-02	2.8	ns	-1.3	ns
solyc02g079500.2.1	9	Suberization-associated anionic peroxidase 1	misc.peroxidases	5.1	2.1E-04	3.8	1.5E-03	3.2	1.1E-02	1.5	ns
solyc05g052280.2.1	9	Peroxidase	misc.peroxidases	3.6	6.8E-03	3.3	2.4E-02	0.4	ns	-0.1	ns
solyc04g071900.2.1	9	Peroxidase	misc.peroxidases	2.8	5.3E-03	3	2.2E-04	2	3.2E-04	1.2	5.1E-02
solyc04g071890.2.1	9	Peroxidase	misc.peroxidases	2.8	1.7E-04	2.4	5.3E-04	2.1	2.1E-03	1.3	3.4E-02
solyc01g095670.2.1	9	Uncharacterized protein	misc.rhodanese	2.6	3.3E-02	2.3	3.5E-03	0.6	ns	0.3	ns
solyc09g090980.2.1	9	PR10 protein	RNA.processing.ribonucleases	2.2	4.0E-04	1.8	2.9E-03	1.3	3.8E-02	0.5	ns
solyc03g098280.2.1	9	Protein argonaute	RNA.regulation of transcription.Argonaute	5.7	1.8E-03	2.5	ns	-0.4	ns	-0.2	ns
solyc06g073530.1.1	9	Protein argonaute	RNA.regulation of transcription.Argonaute	1.9	5.1E-02	1.5	ns	2.8	ns	1.8	ns
solyc01g067790.2.1	9	Uncharacterized protein	RNA.regulation of transcription.unclassified	3.2	2.3E-02	4.4	1.3E-03	3.5	1.1E-02	2.1	ns
solyc05g053780.2.1	9	Uncharacterized protein	RNA.RNA binding	3	3.1E-03	2.5	5.2E-02	2.8	ns	2.4	ns
solyc08g007220.2.1	9	Uncharacterized protein	RNA.RNA binding	6.4	5.1E-02	5.8	5.1E-02	2.9	ns	0.4	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc01g090190.2.1	9	Uncharacterized protein	RNA.RNA binding	2.9	5.0E-02	3.2	5.1E-02	2.9	ns	3.7	ns
solyc02g063130.2.1	9	Uncharacterized protein	DNA.repair	3.4	4.5E-03	2	4.6E-02	1.3	5.0E-02	0.6	ns
solyc04g007120.2.1	9	Uncharacterized protein	DNA.repair	6.4	5.0E-02	5.2	4.9E-02	3.9	5.0E-02	2.5	ns
solyc01g066840.2.1	9	40S ribosomal protein S21	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S21	3.3	3.7E-03	1.7	3.5E-05	0.9	3.8E-03	1.5	4.6E-02
solyc06g073430.2.1	9	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S29	2.1	5.1E-02	1.5	ns	0.2	ns	-0.2	ns
solyc06g007670.2.1	9	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L5	3.5	1.5E-03	2.6	1.2E-02	1.7	ns	0.7	ns
solyc06g075180.1.1	9	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L12	2.3	4.2E-04	1	5.1E-02	1	ns	0.4	ns
solyc02g070310.2.1	9	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L32	2.3	5.0E-02	1.4	ns	1.3	ns	-0.1	ns
solyc07g009330.2.1	9	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.unknown	3.8	4.8E-02	3.1	4.1E-02	2.2	ns	1.5	ns
solyc03g112360.1.1	9	Uncharacterized protein	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L27A	2.3	ns	1.5	ns	2.3	ns	0.2	ns
solyc00g007270.2.1	9	Eukaryotic translation initiation factor 6	protein.synthesis.initiation	3.6	1.5E-03	1.2	ns	1.4	ns	-0.7	ns
solyc01g060470.2.1	9	Importin subunit alpha	protein.targeting.nucleus	6.1	5.0E-02	3.6	ns	2.8	5.1E-02	1.9	ns
solyc09g031780.2.1	9	Uncharacterized protein	protein.targeting.chloroplast	4.9	5.1E-02	4	ns	3.5	ns	3.2	ns
solyc04g007100.2.1	9	Uncharacterized protein	protein.postranslational modification	2.4	5.4E-03	1.2	ns	0.7	ns	0.5	ns
solyc05g009600.2.1	9	Uncharacterized protein	protein.postranslational modification	2.4	1.7E-02	1.2	ns	0.7	ns	0.5	ns
solyc06g069180.2.1	9	Uncharacterized protein	protein.postranslational modification	2.4	5.4E-03	1.2	ns	0.7	ns	0.5	ns
solyc11g066590.1.1	9	Uncharacterized protein	protein.degradation	3.4	3.4E-03	2.8	1.7E-02	1.8	ns	0.3	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc02g091580.2.1	9	Uncharacterized protein	protein.degradation	2.3	1.2E-02	2.3	8.4E-03	1.1	ns	0.3	ns
solyc02g077040.2.1	9	Uncharacterized protein	protein.degradation.cysteine protease	2.2	3.1E-03	1.3	5.1E-02	2.3	3.7E-03	0.5	ns
solyc04g080880.2.1	9	Uncharacterized protein	protein.degradation.cysteine protease	6.2	5.0E-02	5.1	5.0E-02	3.3	ns	-0.6	ns
solyc07g051850.2.1	9	Uncharacterized protein	protein.degradation.aspartate protease	2.6	2.3E-03	1.9	5.8E-04	1.7	2.1E-05	0.2	ns
solyc03g112590.2.1	9	Uncharacterized protein	protein.degradation.AAA type	1.8	3.1E-02	0.8	ns	1.7	ns	-0.2	ns
solyc03g082630.2.1	9	Uncharacterized protein	protein.degradation.AAA type	3	5.1E-02	2.6	5.0E-02	2.8	ns	1	ns
solyc06g053160.2.1	9	Uncharacterized protein	protein.degradation.AAA type	3	5.0E-02	2.6	5.0E-02	2.8	ns	1	ns
solyc03g112590.2.1	9	Uncharacterized protein	protein.degradation.ubiquitin.proteasom	1.8	3.1E-02	0.8	ns	1.7	ns	-0.2	ns
solyc10g077030.1.1	9	Proteasome subunit alpha type	protein.degradation.ubiquitin.proteasom	2.3	5.7E-04	0.9	5.0E-02	1.1	ns	0.3	ns
solyc06g082630.2.1	9	Uncharacterized protein	protein.degradation.ubiquitin.proteasom	3	5.1E-02	2.6	5.1E-02	2.8	ns	1	ns
solyc02g081700.1.1	9	Proteasome subunit alpha type	protein.degradation.ubiquitin.proteasom	3.6	2.3E-02	2.8	4.9E-02	2.2	5.0E-02	1.9	ns
solyc02g070510.2.1	9	Proteasome subunit alpha type	protein.degradation.ubiquitin.proteasom	4.9	5.1E-02	5.2	5.1E-02	3.4	ns	1.5	ns
solyc05g018590.2.1	9	Uncharacterized protein	protein.degradation.ubiquitin.proteasom	3	5.1E-02	2.6	5.1E-02	2.8	ns	1	ns
solyc01g099760.2.1	9	26S protease regulatory subunit 6A homolog	protein.degradation.ubiquitin.proteasom	3	5.1E-02	2.6	5.0E-02	2.8	ns	1	ns
solyc07g016200.2.1	9	Proteasome subunit beta type	protein.degradation.ubiquitin.proteasom	4	1.3E-03	2.8	6.6E-05	2.5	5.8E-03	0.8	ns
solyc02g085790.2.1	9	Uncharacterized protein	protein.folding	4.7	3.0E-03	2.9	ns	0.3	ns	2.2	ns
solyc05g010240.2.1	9	Uncharacterized protein	protein.folding	3.1	7.0E-07	1.9	1.2E-02	0.2	ns	-0.1	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc01g105410.2.1	9	Uncharacterized protein	signalling.in sugar and nutrient physiology	3.9	8.2E-05	3.8	1.2E-04	2.8	3.4E-03	0.9	ns
solyc03g118040.2.1	9	Calnexin-like protein	signalling.calcium	1.9	1.3E-02	1.7	2.0E-02	1.6	4.0E-02	0.7	ns
solyc05g056230.2.1	9	Uncharacterized protein	signalling.calcium	3	5.0E-02	4.6	3.7E-03	3.8	ns	2.7	ns
solyc11g005910.1.1	9	Uncharacterized protein	signalling.phosphinositides.phosphatidylinositol 4-kinase	2.7	5.0E-02	1.6	ns	0	ns	-0.4	ns
solyc12g008590.1.1	9	Profilin	cell.organisation	3.6	3.5E-02	3.4	3.9E-02	1.3	5.1E-02	0.8	ns
solyc04g081490.2.1	9	Beta-tubulin	cell.organisation	2	1.6E-02	2.4	7.1E-03	2	3.9E-02	1.2	ns
solyc04g055170.2.1	9	Annexin	cell.organisation	4.7	2.3E-02	4.1	3.1E-02	3.5	ns	2.1	ns
solyc10g080940.1.1	9	Uncharacterized protein	cell.organisation	1.7	3.6E-02	2.1	1.4E-02	1.7	ns	1.1	ns
solyc04g073990.2.1	9	Annexin	cell.organisation	3.8	2.0E-07	3.1	2.5E-06	1.9	5.3E-04	1	5.0E-02
solyc04g077020.2.1	9	Uncharacterized protein	cell.organisation	1.8	1.7E-03	1.9	1.6E-03	2.2	1.5E-03	1.6	9.7E-03
solyc08g066110.2.1	9	Profilin-2	cell.organisation	2.7	1.9E-05	1.6	1.4E-03	0.7	ns	0.5	ns
solyc11g010920.1.1	9	Kinesin-like protein	cell.organisation	2.5	4.7E-06	2.1	2.4E-05	1.5	1.4E-03	1.1	2.2E-02
solyc03g112590.2.1	9	Uncharacterized protein	cell.division	1.8	3.1E-02	0.8	ns	1.7	ns	-0.2	ns
solyc11g006070.1.1	9	Peptidyl-prolyl cis-trans isomerase	cell.cycle.peptidylprolyl isomerase	2.7	1.4E-04	1.9	3.8E-03	1.3	ns	0.1	ns
solyc06g083190.2.1	9	Uncharacterized protein	cell.cycle.peptidylprolyl isomerase	3.2	5.0E-02	1.8	5.0E-02	1.3	ns	-1.6	ns
solyc06g076970.2.1	9	Peptidyl-prolyl cis-trans isomerase	cell.cycle.peptidylprolyl isomerase	2.8	7.8E-05	0.8	5.1E-02	0.5	ns	0.1	ns
solyc02g069150.2.1	9	Uncharacterized protein	cell.vesicle transport	3.9	6.8E-03	1.7	ns	0.8	ns	-0.4	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc09g061620.2.1	9	Uncharacterized protein	cell.vesicle transport	3.9	6.8E-03	1.7	ns	0.8	ns	-0.4	ns
solyc02g069590.2.1	9	Uncharacterized protein	cell.vesicle transport	5.6	5.0E-02	3.1	5.0E-02	4.1	5.0E-02	4.1	ns
solyc09g091610.2.1	9	Uncharacterized protein	cell.vesicle transport	3.9	6.8E-03	1.7	ns	0.8	ns	-0.4	ns
solyc01g110120.2.1	9	V-type proton ATPase subunit a	transport.p- and v-ATPases	1.9	2.2E-04	1.5	8.8E-04	0.8	ns	-0.2	ns
solyc00g164680.1.1	9	Uncharacterized protein	transport.ABC transporters and multidrug resistance systems	1.6	ns	2.2	2.3E-02	1	ns	-0.4	ns
solyc06g074820.2.1	9	Similar to aquaporin	transport.Major Intrinsic Proteins.TIP	1.3	4.9E-02	3.6	ns	2.6	ns	0.9	ns
solyc05g013850.2.1	9	Uncharacterized protein	not assigned.unknown	1.9	1.2E-02	1.9	3.7E-02	2.9	1.7E-03	0.6	ns
solyc06g071050.2.1	9	Uncharacterized protein	not assigned.unknown	1.9	1.6E-04	1.2	4.4E-03	1.4	6.8E-03	0.2	ns
solyc06g076480.2.1	9	Uncharacterized protein	not assigned.unknown	3.9	2.1E-02	3	5.1E-02	-0.5	ns	1.4	ns
solyc04g016360.2.1	9	Uncharacterized protein	not assigned.unknown	3.7	1.6E-02	2.2	ns	1.6	ns	0.9	ns
solyc06g073900.2.1	9	Uncharacterized protein	not assigned.unknown	4.2	5.0E-04	2.8	1.0E-02	1.7	ns	2.1	ns
solyc05g013870.2.1	9	Uncharacterized protein	not assigned.unknown	1.5	4.8E-02	1.3	ns	2.6	3.7E-02	0.4	ns
solyc02g014550.1.1	9	Uncharacterized protein	not assigned.unknown	2.7	5.1E-02	1.6	ns	0	ns	-0.4	ns
solyc04g072240.2.1	9	Uncharacterized protein	not assigned.unknown	3.4	5.2E-04	1.5	ns	0.6	ns	0.4	ns
solyc09g075010.2.1	9	Uncharacterized protein	not assigned.unknown	3.6	6.7E-04	2	5.0E-02	1.1	ns	0.8	ns
solyc04g039600.1.1	9	Uncharacterized protein	not assigned.unknown	2.7	5.1E-02	1.6	ns	0	ns	-0.4	ns
solyc03g063410.1.1	9	Uncharacterized protein	not assigned.unknown	2.7	5.0E-02	1.6	5.1E-02	0	ns	-0.4	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc03g079930.2.1	9	Uncharacterized protein	not assigned.unknown	3.2	2.3E-02	4.4	1.3E-03	3.5	1.1E-02	2.1	ns
solyc02g088260.2.1	9	Uncharacterized protein	not assigned.unknown	3.6	3.1E-05	2.3	1.1E-03	1.7	1.7E-02	1	ns
solyc01g010750.2.1	9	Uncharacterized protein	not assigned.unknown	3.2	5.0E-02	4	5.0E-02	2.7	ns	2.2	ns
solyc03g111810.2.1	9	Uncharacterized protein	not assigned.unknown	1.2	5.1E-02	3.7	5.0E-02	5.2	6.0E-02	4.1	ns
solyc06g064910.2.1	9	Uncharacterized protein	not assigned.unknown	2.8	5.4E-02	1.8	5.0E-02	0.6	ns	-0.8	ns
solyc03g113220.2.1	9	Uncharacterized protein	not assigned.unknown	1.8	3.2E-04	1.3	3.8E-03	1.4	5.2E-03	0.2	ns
solyc07g007760.2.1	9	Uncharacterized protein	not assigned.unknown	5.3	2.0E-04	4.2	4.6E-06	3.7	2.0E-05	1.3	ns
solyc04g026020.2.1	9	Uncharacterized protein	not assigned.unknown	3.2	2.5E-04	2.9	2.1E-03	3.9	1.2E-04	1.3	ns
solyc01g106090.2.1	10	Uncharacterized protein	PS.lightreaction.photosystem II.PSII polypeptide subunits	10	4.2E-03	10	5.0E-02	10	5.0E-02	10	ns
solyc02g011760.1.1	10	Uncharacterized protein	PS.lightreaction.photosystem I.PSI polypeptide subunits	10	8.9E-06	10	4.0E-05	10	5.0E-02	10	ns
solyc07g043570.2.1	10	Uncharacterized protein	minor CHO metabolism.others	10	1.4E-02	10	ns	10	ns	10	ns
solyc04g005160.1.1	10	6-phosphogluconate dehydrogenase, decarboxylating	OPP.oxidative PP.6-phosphogluconate dehydrogenase	10	8.8E-05	10	ns	10	ns	10	ns
solyc12g005080.1.1	10	Uncharacterized protein	TCA / org. transformation.TCA.pyruvate DH.E2	10	8.2E-03	10	ns	10	ns	10	ns
solyc12g005080.1.1	10	Uncharacterized protein	TCA / org. transformation.TCA.2-oxoglutarate dehydrogenase	10	8.2E-03	10	ns	10	ns	10	ns
solyc05g005160.2.1	10	Uncharacterized protein	TCA / org. transformation.other organic acid transformaitons.atp-citrate lyase	10	2.1E-02	10	ns	10	ns	10	ns
solyc05g007830.2.1	10	Uncharacterized protein	cell wall.modification	10	4.0E-04	10	1.5E-02	10	ns	10	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM_fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc07g055210.2.1	10	Aspartate aminotransferase	amino acid metabolism.synthesis.central amino acid metabolism.aspartate.aspartate aminotransferase	10	5.7E-03	10	ns	10	ns	10	ns
solyc04g074480.2.1	10	Uncharacterized protein	amino acid metabolism.synthesis.aromatic aa.chorismate.3-deoxy-D-arabino-heptulosonate 7-phosphate synthase	10	3.9E-04	10	1.5E-02	10	ns	10	ns
solyc09g005500.2.1	10	Uncharacterized protein	stress.abiotic.unspecified	10	1.4E-04	10	2.5E-02	10	ns	10	ns
solyc10g080190.1.1	10	Uncharacterized protein	stress.abiotic.unspecified	10	1.4E-02	10	ns	10	ns	10	ns
solyc03g044790.2.1	10	Methylesterase	misc.nitrilases, *nitrile lyases, berberine bridge enzymes, reticuline oxidases, troponine reductases	10	5.0E-02	10	7.8E-03	10	5.1E-02	10	ns
solyc12g013900.1.1	10	Uncharacterized protein	misc.plastocyanin-like	10	5.0E-02	10	ns	10	ns	10	ns
solyc02g071700.2.1	10	Uncharacterized protein	misc.GDSL-motif lipase	10	6.6E-03	10	4.9E-02	10	ns	10	ns
solyc10g081370.1.1	10	Small nuclear ribonucleoprotein F	RNA.processing	10	1.4E-02	10	ns	10	ns	10	ns
solyc09g091000.2.1	10	Uncharacterized protein	RNA.processing.ribonucleases	10	2.1E-04	10	1.5E-02	10	ns	10	ns
solyc01g104840.2.1	10	Uncharacterized protein	RNA.RNA binding	10	4.9E-02	10	0.0E+00	10	6.5E-03	10	ns
solyc10g051340.1.1	10	Adenylyl cyclase-associated protein	DNA.unspecified	10	1.5E-02	10	ns	10	ns	10	ns
solyc06g068320.2.1	10	Uncharacterized protein	protein.aa activation.bifunctional aminoacyl-tRNA synthetase	10	7.2E-03	10	4.8E-02	10	ns	10	ns
solyc03g120630.2.1	10	Uncharacterized protein	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.30S subunit.S17	10	1.7E-03	10	4.2E-03	10	ns	10	ns
solyc06g052030.2.1	10	Uncharacterized protein	protein.targeting.nucleus	10	6.1E-04	10	ns	10	ns	10	ns
solyc08g078250.2.1	10	Uncharacterized protein	protein.postranslational modification	10	1.5E-02	10	ns	10	ns	10	ns

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Table A.2. (cont.)

ID	Cluster	Description	MAPMAN Category	T6homo/MM fold	T6homo/MM_P val	T19homo/MM_fold	T19homo/MM_P val	T6hemi/MM_fold	T6hemi/MM_P val	T19hemi/MM_fold	T19hemi/MM_P val
solyc11g072710.1.1	10	Uncharacterized protein	protein.postranslational modification	10	4.6E-02	10	ns	10	ns	10	ns
solyc02g076980.2.1	10	Cysteine protease	protein.degradation.cysteine protease	10	4.1E-02	10	4.7E-02	10	ns	10	ns
solyc01g007860.2.1	10	Uncharacterized protein	protein.degradation.ubiquitin.E2	10	3.4E-04	10	9.4E-04	10	5.4E-03	10	ns
solyc02g084920.2.1	10	Proteasome subunit beta type	protein.degradation.ubiquitin.proteasom	10	5.1E-02	10	ns	10	ns	10	ns
solyc01g088080.2.1	10	Uncharacterized protein	protein.folding	10	7.4E-03	10	5.0E-02	10	ns	10	ns
solyc03g118810.1.1	10	Uncharacterized protein	signalling.calcium	10	5.3E-03	10	ns	10	ns	10	ns
solyc03g083970.2.1	10	Uncharacterized protein	signalling.calcium	10	3.2E-04	10	1.5E-02	10	ns	10	ns
solyc04g078380.1.1	10	MFP1 attachment factor 1	cell.organisation	10	6.8E-03	10	5.2E-02	10	ns	10	ns
solyc06g074650.2.1	10	Uncharacterized protein	cell.vesicle transport	10	5.0E-03	10	ns	10	4.9E-02	10	ns
solyc12g009890.1.1	10	Uncharacterized protein	transport.p- and v-ATPases.H+-transporting two-sector ATPase.subunit H	10	6.8E-04	10	ns	10	ns	10	ns

Table A. 3. List of proteins differentially regulated in transgenic and nontransgenic plants grown under drought stress condition from leaf total protein extract.

ID	Cluster	Description	MAPMAN Category	*SARK::IPTs/ SARK::IPTc*	Pval_SARK::IPT	MMs/ MMc	Pval_MM
solyc12g011450.1.1	1	Chlorophyll a-b binding protein 13. chloroplastic	PS.lightreaction.photosystem II.LHC-II	1.13	1.53E-06	-0.36	ns
solyc01g105030.2.1	1	Chlorophyll a-b binding protein. chloroplastic	PS.lightreaction.photosystem II.LHC-II	1.74	1.50E-07	-0.21	ns
solyc02g071000.1.1	1	Chlorophyll a-b binding protein	PS.lightreaction.photosystem II.LHC-II	0.68	1.58E-04	-0.16	ns
solyc03g005780.1.1	1	Chlorophyll a-b binding protein 3C-like	PS.lightreaction.photosystem II.LHC-II	1.83	1.15E-05	-0.74	8.73E-03
solyc06g063370.2.1	1	Chlorophyll a-b binding protein 1A. chloroplastic	PS.lightreaction.photosystem II.LHC-II	0.92	9.81E-03	-0.41	1.65E-02
solyc12g011280.1.1	1	Chlorophyll a-b binding protein 8. chloroplastic	PS.lightreaction.photosystem II.LHC-II	2.25	5.00E-08	0.2	ns
solyc02g079950.2.1	1	Oxygen-evolving enhancer protein 3	PS.lightreaction.photosystem II.PSII polypeptide subunits	2.25	2.69E-06	-0.32	1.52E-02
solyc06g065490.2.1	1	PsbP domain-containing protein 6. chloroplastic	PS.lightreaction.photosystem II.PSII polypeptide subunits	1.53	4.71E-04	0.24	ns
solyc01g087040.2.1	1	Thylakoid lumenal 19 kDa protein. chloroplastic	PS.lightreaction.photosystem II.PSII polypeptide subunits	2.44	1.84E-04	0.19	ns
solyc06g082940.2.1	1	Photosystem I reaction center subunit XI	PS.lightreaction.photosystem I.PSI polypeptide subunits	1.59	5.01E-06	-0.34	ns
solyc08g013670.2.1	1	Photosystem I reaction center subunit	PS.lightreaction.photosystem I.PSI polypeptide subunits	1.24	3.31E-05	-0.26	ns
solyc03g120640.2.1	1	Photosystem I reaction center subunit VI-1. chloroplastic	PS.lightreaction.photosystem I.PSI polypeptide subunits	1.48	2.26E-04	-0.27	ns
solyc09g090570.2.1	1	Proton gradient regulation 5	PS.lightreaction.cyclic electron flow-chlororespiration	2.19	1.55E-06	-0.16	ns
solyc02g085950.2.1	1	Ribulose bisphosphate carboxylase small chain	PS.calvin cycle.rubisco small subunit	1.95	1.00E-08	-0.62	ns
solyc03g115820.2.1	1	Ribulose-5-phosphate-3-epimerase	PS.calvin cycle.RPE	0.29	ns	-0.58	5.17E-04
solyc06g073190.2.1	1	Fructokinase-like	major CHO metabolism.degradation.sucrose.fructokinase	0.89	4.78E-02	0.22	ns

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Table A.3. (cont.)

ID	Cluster	Description	MAPMAN Category	*SARK::IPTs/ SARK::IPTc*	Pval_SARK::IPT	MMs/ MMc	Pval_MM
solyc01g097460.2.1	1	Ribose-5-phosphate isomerase	OPP.non-reductive PP.ribose 5-phosphate isomerase	0.57	ns	-0.49	4.27E-03
solyc07g006790.2.1	1	Dihydrolipoyllysine-residue acetyltransferase component of pyruvate dehydrogenase complex	TCA / org. transformation.TCA.pyruvate DH.E2	0.91	9.57E-04	-0.11	ns
solyc02g086820.2.1	1	Carbonic anhydrase	TCA / org. transformation.carbonic anhydrases	0.91	4.34E-06	-0.31	ns
solyc10g008140.2.1	1	Prohibitin 1-like protein	mitochondrial electron transport / ATP synthesis.NADH-DH.complex I	1.44	ns	0.27	ns
solyc01g112000.2.1	1	Expansin-like protein	cell wall.modification	1.28	1.65E-05	-0.05	ns
solyc11g069040.2.1	1	Lactoylglutathione lyase	amino acid metabolism.degradation.aspartate family.threonine	1.39	1.58E-05	0.63	3.73E-04
solyc09g090430.2.1	1	Cyanate hydratase	secondary metabolism.N misc.cyanogenic glycosides	0.96	1.40E-03	0.09	ns
solyc09g014760.2.1	1	Chlorophyll synthase	tetrapyrrole synthesis.chlorophyll synthase	0.88	6.72E-03	-0.07	ns
solyc08g080640.1.1	1	Osmotin-like protein (Fragment)	stress.biotic	1.16	3.35E-03	0.57	ns
solyc04g005700.2.1	1	Major latex-like protein	stress.abiotic.unspecified	0.95	1.14E-04	0.22	ns
solyc12g013810.1.1	1	Thioredoxin	redox.thioredoxin	0.9	3.61E-05	-0.4	1.56E-03
solyc10g078920.1.1	1	Thioredoxin-like 5	redox.thioredoxin	0.64	7.33E-04	-0.59	7.30E-04
solyc10g006970.2.1	1	Thioredoxin m	redox.thioredoxin	1.29	3.96E-06	-0.27	ns
solyc07g063190.2.1	1	Thioredoxin	redox.thioredoxin	1.11	1.33E-04	0.15	ns
solyc12g056230.1.1	1	Glutathione peroxidase	redox.ascorbate and glutathione.glutathione	1.53	1.67E-03	0.07	ns
solyc08g006720.2.1	1	Glutathione peroxidase	redox.ascorbate and glutathione.glutathione	1.93	2.60E-07	-0.33	ns
solyc06g005260.2.1	1	Cytoplasmic glutaredoxin thioltransferase glutathione-dependent disulfide oxidoreductase	redox.glutaredoxins	0.93	9.99E-05	-0.22	ns
solyc07g042440.2.1	1	Alkyl hydroperoxide reductase	redox.peroxiredoxin	0.89	9.74E-06	0.23	ns
solyc10g082030.1.1	1	Peroxiredoxin	redox.peroxiredoxin.BAS1	0.74	3.09E-02	-0.05	ns
solyc01g007740.2.1	1	Peroxiredoxin	redox.peroxiredoxin.BAS1	0.77	2.49E-03	0.13	ns
solyc06g048410.2.1	1	Superoxide dismutase	redox.dismutases and catalases	1.45	1.64E-03	-0.53	2.83E-04

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Table A.3. (cont.)

ID	Cluster	Description	MAPMAN Category	*SARK::IPTs/ SARK::IPTc*	Pval_SARK::IPT	MMs/ MMc	Pval_MM
solyc06g049080.2.1	1	Superoxide dismutase	redox.dismutases and catalases	1.02	3.78E-03	0.13	ns
solyc12g094430.1.1	1	Glutathione S-transferase	misc.glutathione S transferases	0.98	4.94E-05	-0.23	ns
solyc06g009020.2.1	1	Glutathione S-transferase	misc.glutathione S transferases	1.48	4.43E-06	0.19	ns
solyc05g049950.2.1	1	Small nuclear ribonucleoprotein-associated protein B	RNA.processing	0.97	ns	0.08	ns
solyc06g073540.2.1	1	Argonaute 4-like protein	RNA.regulation of transcription.Argonaute	0.87	4.73E-05	-0.4	3.38E-03
solyc02g086730.1.1	1	50S ribosomal protein L12-C	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.50S subunit.L12	0.89	1.42E-03	0.33	ns
solyc08g006040.2.1	1	40S ribosomal protein S6	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S6	1.52	8.78E-05	0.03	ns
solyc01g060470.2.1	1	Importin alpha-1b subunit	protein.targeting.nucleus	0.5	4.46E-03	-0.16	ns
solyc08g076970.2.1	1	Acetylornithine deacetylase or succinyl-diaminopimelate desuccinylase	protein.degradation	1	2.95E-04	0.54	ns
solyc01g100520.2.1	1	ATP-dependent Clp protease proteolytic subunit	protein.degradation.serine protease	0.95	6.06E-04	0	ns
solyc09g090330.2.1	1	Harpin binding protein 1	cell.organisation	0.51	ns	0.13	ns
solyc11g044530.1.1	1	PAP fibrillin	cell.organisation	2.25	1.74E-02	-0.64	9.13E-03
solyc02g077880.2.1	1	Auxin-repressed protein	development.unspecified	1.69	1.65E-05	0.51	2.19E-05
solyc01g096240.2.1	1	Homology to unknown gene	not assigned.unknown	1.12	4.11E-02	-0.37	ns
solyc04g054980.2.1	1	Lipoxygenase homology domain-containing protein 1	not assigned.unknown	1.68	7.73E-05	0.19	ns
solyc01g006900.2.1	1	Phosphatidylglycerol	not assigned.unknown	0.9	8.69E-03	0.47	6.93E-04
solyc11g022590.1.1	1	Kunitz trypsin inhibitor 4 (Fragment)	not assigned.unknown	0.86	1.36E-04	-3.15	1.56E-02
solyc10g075100.1.1	2	Non-specific lipid-transfer protein	lipid metabolism.lipid transfer proteins etc	4.51	3.33E-06	2.74	1.28E-03
solyc05g015390.2.1	2	REF-like stress related protein 1	secondary metabolism.isoprenoids	2.26	9.43E-04	1.58	2.04E-05
solyc04g080850.2.1	2	Thioredoxin	redox.thioredoxin	2.35	1.33E-02	0.98	2.67E-05
solyc12g013900.1.1	2	CT099 (Fragment)	misc.plastocyanin-like	2.2	4.54E-04	1.83	4.18E-03

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Table A.3. (cont.)

ID	Cluster	Description	MAPMAN Category	*SARK::IPTs/ SARK::IPTc*	Pval_SARK::IPT	MMs/ MMc	Pval_MM
solyc07g064600.2.1	2	Endoribonuclease L-PSP family protein	RNA.processing.ribonucleases	3.04	1.01E-06	1.11	3.76E-02
solyc03g019820.2.1	2	Aquaporin	transport.Major Intrinsic Proteins.TIP	6.34	7.54E-05	3.25	3.82E-06
solyc09g092710.2.1	2	Glycine rich protein	not assigned.unknown	2.09	2.55E-06	1.13	2.61E-06
solyc04g071620.2.1	2	ASR4 (Fragment)	not assigned.unknown	2.48	5.16E-04	2.01	5.92E-05
solyc01g011480.1.1	3	Photosystem II CP43 chlorophyll apoprotein	PS.lightreaction.photosystem II.PSII polypeptide subunits	-2.04	1.63E-04	-0.26	ns
solyc02g065400.2.1	3	Oxygen-evolving enhancer protein 1 of photosystem II	PS.lightreaction.photosystem II.PSII polypeptide subunits	-0.99	4.30E-07	-0.1	ns
solyc00g230080.1.1	3	Photosystem II D2 protein	PS.lightreaction.photosystem II.PSII polypeptide subunits	-0.77	1.81E-05	-0.28	ns
solyc01g011410.1.1	3	NADH-quinone oxidoreductase subunit D	PS.lightreaction.cyclic electron flow-chlororespiration	-0.68	2.10E-04	0.05	ns
solyc12g099930.1.1	3	Serine-glyoxylate aminotransferase	PS.photorespiration.aminotransferases peroxisomal	-1.2	1.20E-03	-0.91	9.75E-06
solyc08g065490.2.1	3	Serine hydroxymethyltransferase	PS.photorespiration.serine hydroxymethyltransferase	-0.65	1.04E-03	-0.3	ns
solyc02g091560.2.1	3	Serine hydroxymethyltransferase	PS.photorespiration.serine hydroxymethyltransferase	-0.79	1.04E-03	-0.7	1.47E-06
solyc01g111630.2.1	3	Glyoxylate	PS.photorespiration.hydroxypyruvate reductase	-1.11	5.06E-05	-0.66	5.02E-04
solyc07g066600.2.1	3	Phosphoglycerate kinase	PS.calvin cycle.phosphoglycerate kinase	-1.16	1.84E-02	-0.33	ns
solyc06g071920.2.1	3	Glyceraldehyde-3-phosphate dehydrogenase	glycolysis.cytosolic branch.glyceraldehyde 3-phosphate dehydrogenase (GAP-DH)	-1.02	6.55E-04	0.04	ns
solyc01g106480.2.1	3	Malate dehydrogenase	gluconeogenesis.Malate DH	-1.32	2.01E-04	-0.89	1.31E-03
solyc12g009400.1.1	3	Pyruvate dehydrogenase E1 component alpha subunit E1 component. alpha subunit. subgroup	TCA / org. transformation.TCA.pyruvate DH.E1	-1.13	2.12E-04	-0.64	1.25E-05
solyc05g009530.2.1	3	Dihydrolipoyllysine-residue acetyltransferase component of pyruvate dehydrogenase complex	TCA / org. transformation.TCA.pyruvate DH.E2	-0.85	1.74E-04	-0.33	ns
solyc05g053100.2.1	3	Dihydrolipoyl dehydrogenase	TCA / org. transformation.TCA.pyruvate DH.E3	-0.58	5.08E-04	-0.47	1.42E-03
solyc03g122310.2.1	3	Aldehyde dehydrogenase 7b	TCA / org. transformation.other organic acid transformaitons.misc	-1.47	3.89E-04	-0.79	9.02E-06

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Table A.3. (cont.)

ID	Cluster	Description	MAPMAN Category	*SARK::IPTs/ SARK::IPTc*	Pval_SARK::IPT	MMs/ MMc	Pval_MM
solyc07g053540.1.1	3	Fasciclin-like arabinogalactan protein 4	cell wall.cell wall proteins.AGPs.AGP	-0.85	5.22E-03	0.39	ns
solyc01g008330.2.1	3	Acetyl-CoA carboxylase biotin carboxylase	lipid metabolism.FA synthesis and FA elongation.Acetyl CoA Carboxylation.heteromeric Complex.Biotin Carboxylase	-1.39	2.77E-04	-0.21	ns
solyc08g082280.2.1	3	Long-chain-fatty-acid-CoA ligase	lipid metabolism.FA synthesis and FA elongation.long chain fatty acid CoA ligase	-1.44	8.62E-05	-0.47	ns
solyc03g118410.2.1	3	Acyl carrier protein	lipid metabolism.FA synthesis and FA elongation.ACP protein	-0.57	1.41E-04	0.06	ns
solyc01g108630.2.1	3	Nitrite reductase	N-metabolism.nitrate metabolism.nitrite reductase	-1.14	3.35E-05	-0.71	2.57E-05
solyc12g099930.1.1	3	Serine-glyoxylate aminotransferase	amino acid metabolism.synthesis.central amino acid metabolism.alanine.alanine-glyoxylate aminotransferase	-1.2	1.20E-03	-0.91	9.75E-06
solyc12g089210.1.1	3	Ornithine carbamoyltransferase	amino acid metabolism.synthesis.glutamate family.arginine.ornithine carbamoyltransferase	-0.79	7.23E-04	-0.74	3.20E-04
solyc10g081510.1.1	3	5-methyltetrahydropteroyltriglutamate--homocysteine methyltransferase	amino acid metabolism.synthesis.aspartate family.methionine	-1.28	4.76E-04	0.15	ns
solyc09g008280.1.1	3	S-adenosylmethionine synthase	amino acid metabolism.synthesis.aspartate family.methionine	-0.89	3.09E-05	-0.4	1.52E-03
solyc01g109850.2.1	3	Diaminopimelate decarboxylase	amino acid metabolism.synthesis.aspartate family.lysine.diaminopimelate decarboxylase	-0.79	2.42E-04	0.01	ns
solyc07g053280.2.1	3	Ketol-acid reductoisomerase	amino acid metabolism.synthesis.branched chain group.common	-0.82	2.01E-03	-0.16	ns
solyc01g091160.2.1	3	Agmatinase	amino acid metabolism.degradation.glutamate family.arginine	-0.78	4.35E-03	0.37	ns
solyc03g005260.2.1	3	Sulfate adenylyltransferase	S-assimilation.ATPS	-1.98	1.99E-04	-1.24	1.18E-04
solyc03g115980.1.1	3	Geranylgeranyl reductase	secondary metabolism.isoprenoids.non-mevalonate pathway	-1.78	1.07E-02	-1.11	2.18E-03
solyc03g114340.2.1	3	1-deoxy-D-xylulose-5-phosphate reductoisomerase	secondary metabolism.isoprenoids.non-mevalonate pathway.DXR	-1.08	6.55E-03	-1.04	1.70E-07
solyc11g069380.1.1	3	4-hydroxy-3-methylbut-2-en-1-yl diphosphate synthase	secondary metabolism.isoprenoids.non-mevalonate pathway.HDS	-1.37	2.65E-04	-0.51	5.69E-03
solyc03g025320.2.1	3	Hydroxycinnamoyl transferase	secondary metabolism.phenylpropanoids	-1.27	5.21E-04	-0.71	4.20E-07

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Table A.3. (cont.)

ID	Cluster	Description	MAPMAN Category	*SARK::IPTs/ SARK::IPTc*	Pval_SARK::IPT	MMs/ MMc	Pval_MM
solyc02g090890.2.1	3	Zeaxanthin epoxidase. chloroplastic	hormone metabolism.abscisic acid.synthesis-degradation.synthesis.zeaxanthin epoxidase	-0.85	1.74E-03	-0.4	2.18E-02
solyc02g030170.2.1	3	FAD linked oxidase domain protein	hormone metabolism.brassinosteroid.synthesis-degradation.sterols.DWF1	-1	1.07E-04	0.35	ns
solyc05g053340.2.1	3	Gibberellin 2-oxidase	hormone metabolism.ethylene.synthesis-degradation	-0.48	1.97E-02	-0.53	1.44E-04
solyc05g053340.2.1	3	Gibberellin 2-oxidase	hormone metabolism.gibberelin.synthesis-degradation.GA2 oxidase	-0.48	1.97E-02	-0.53	1.44E-04
solyc11g069800.1.1	3	cytochrome P452	hormone metabolism.jasmonate.synthesis-degradation.allene oxidase synthase	-1.43	3.07E-06	-0.38	ns
solyc04g009200.2.1	3	Glutamate-1-semialdehyde-2 1-aminomutase	tetrapyrrole synthesis.GSA	-0.71	3.84E-05	-0.42	1.54E-05
solyc10g008740.2.1	3	Magnesium chelatase ATPase subunit I	tetrapyrrole synthesis.magnesium chelatase	-1.57	2.56E-04	-1.23	1.21E-06
solyc03g118240.2.1	3	Magnesium-protoporphyrin ix methyltransferase	tetrapyrrole synthesis.magnesium protoporphyrin IX methyltransferase	-1.17	4.20E-05	-0.56	5.58E-05
solyc10g077040.1.1	3	Magnesium-protoporphyrin IX monomethyl ester	tetrapyrrole synthesis.magnesium-protoporphyrin IX monomethyl ester (oxidative) cyclase	-2.26	1.87E-05	-1.79	3.00E-08
solyc01g067290.2.1	3	-	tetrapyrrole synthesis.divinyl chlorophyllide-a 8-vinyl-reductase	-1.47	9.09E-05	-0.65	6.29E-05
solyc12g013710.1.1	3	Protochlorophyllide reductase	tetrapyrrole synthesis.protochlorophyllide reductase	-3.54	4.00E-07	-2.15	7.22E-05
solyc07g054210.2.1	3	Protochlorophyllide reductase like protein	tetrapyrrole synthesis.protochlorophyllide reductase	-1.84	4.80E-07	-1.35	5.40E-07
solyc10g047320.1.1	3	Cc-nbs-lrr. resistance protein	stress.biotic	-0.52	6.32E-04	-0.22	ns
solyc10g055200.1.1	3	Disease resistance response	stress.biotic.PR-proteins	-1.42	1.13E-04	-0.6	9.52E-05
solyc09g010630.2.1	3	heat shock protein	stress.abiotic.heat	-1.66	1.11E-04	-0.11	ns
solyc01g106210.2.1	3	Chaperone DnaK	stress.abiotic.heat	-0.75	5.86E-05	0.33	ns
solyc03g082920.2.1	3	Heat shock protein	stress.abiotic.heat	-1.22	4.00E-04	0.01	ns
solyc07g065840.2.1	3	Heat shock protein 90	stress.abiotic.heat	-1.23	8.40E-03	0.39	ns
solyc04g007790.2.1	3	Major latex-like protein	stress.abiotic.unspecified	-0.25	5.81E-04	-0.74	1.00E-10
solyc04g081970.2.1	3	Thioredoxin	redox.thioredoxin	-0.55	2.01E-04	-0.04	ns

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Table A.3. (cont.)

ID	Cluster	Description	MAPMAN Category	*SARK::IPTs/ SARK::IPTc*	Pval_SARK::IPT	MMs/ MMc	Pval_MM
solyc08g081010.2.1	3	Glutamate-cysteine ligase	redox.ascorbate and glutathione.glutathione	-0.88	1.64E-03	-0.54	ns
solyc02g082760.2.1	3	Catalase	redox.dismutases and catalases	-1.31	2.11E-05	-1.69	1.00E-09
solyc12g094620.1.1	3	Catalase	redox.dismutases and catalases	-1	4.21E-05	-1.22	7.03E-06
solyc06g075340.2.1	3	Carbamoyl-phosphate synthase large chain	nucleotide metabolism.synthesis.pyrimidine.carbamoyl phosphate synthetase	-0.8	1.17E-04	-0.12	ns
solyc08g065490.2.1	3	Serine hydroxymethyltransferase	C1-metabolism.glycine hydroxymethyltransferase	-0.65	1.04E-03	-0.3	ns
solyc01g095620.2.1	3	UDP-glucosyltransferase	misc.UDP glucosyl and glucoronyl transferases	-0.95	7.97E-04	-0.15	ns
solyc04g008310.1.1	3	Glucosyltransferase	misc.UDP glucosyl and glucoronyl transferases	-1	4.06E-03	0.08	ns
solyc01g060020.2.1	3	Beta-glucanase	misc.beta 1,3 glucan hydrolases.glucan endo-1,3-beta-glucosidase	-0.98	6.31E-05	-0.58	5.65E-03
solyc02g079500.2.1	3	Peroxidase	misc.peroxidases	-1.53	1.50E-07	-0.54	6.77E-03
solyc02g093640.2.1	3	3-ketoacyl-CoA reductase 1	misc.short chain dehydrogenase/reductase (SDR)	-0.86	4.52E-03	-0.15	ns
solyc03g025270.2.1	3	rRNA 2	RNA.processing	-1.33	2.10E-03	0.3	ns
solyc08g042050.2.1	3	DEAD-box ATP-dependent RNA helicase 3	RNA.processing.RNA helicase	-1.58	3.02E-03	0.13	ns
solyc01g100570.2.1	3	Nucleolar protein	RNA.regulation of transcription.putative transcription regulator	-1.2	9.53E-04	0.41	3.34E-02
solyc09g007850.2.1	3	RNA-binding protein	RNA.RNA binding	-0.7	9.36E-02	-1.48	4.82E-04
solyc01g109660.2.1	3	Glycine-rich RNA-binding protein	RNA.RNA binding	-0.86	3.49E-05	0.44	3.15E-06
solyc10g086150.1.1	3	Single-stranded DNA binding protein	RNA.RNA binding	-1.67	2.89E-05	-0.67	7.10E-04
solyc04g074750.2.1	3	Polyadenylate-binding protein 1-A	RNA.RNA binding	-1.15	3.34E-03	-1	3.25E-03
solyc10g047130.1.1	3	RNA-binding protein RZ-1	RNA.RNA binding	-0.62	9.45E-04	0.5	1.05E-02
solyc08g074550.2.1	3	Threonyl-tRNA synthetase	protein.aa activation.threonine-tRNA ligase	-0.63	9.74E-03	0.21	ns
solyc10g080710.1.1	3	Asparaginyl-tRNA synthetase 2	protein.aa activation.asparagine-tRNA ligase	-1.21	1.08E-05	0.09	ns
solyc01g007580.2.1	3	30S ribosomal protein S8	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.30S subunit.S8	-1.36	1.57E-05	0.24	ns

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Table A.3. (cont.)

ID	Cluster	Description	MAPMAN Category	*SARK::IPTs/ SARK::IPTc*	Pval_SARK::IPT	MMs/ MMc	Pval_MM
solyc06g073090.2.1	3	Ribosomal subunit interface protein	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.30S subunit.S30A	-0.55	8.65E-05	-0.63	2.94E-06
solyc01g010580.2.1	3	Ribosomal protein	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S9	-0.85	4.05E-03	0.64	3.29E-03
solyc06g009210.2.1	3	Ribosomal protein L19	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L19	-0.66	1.67E-05	0.21	ns
solyc01g099830.2.1	3	60S ribosomal protein L22-2	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L22	-0.96	1.00E-05	-0.76	4.50E-07
solyc08g079180.2.1	3	Elongation factor G	protein.synthesis.elongation	-0.84	2.34E-05	-0.44	5.99E-06
solyc03g082940.2.1	3	Importin subunit beta	protein.targeting.nucleus	-1.45	2.31E-02	-0.06	ns
solyc09g031780.2.1	3	Tic110 family transporter chloroplast inner envelope protein Tic111	protein.targeting.chloroplast	-1.24	3.45E-03	-0.19	ns
solyc08g079870.1.1	3	Subtilisin-like protease	protein.degradation.subtilases	-1.59	7.42E-03	-0.78	4.50E-07
solyc05g054120.1.1	3	Cysteine proteinase inhibitor	protein.degradation.cysteine protease	-0.61	8.02E-04	-0.26	ns
solyc01g079940.2.1	3	Xylanase inhibitor (Fragment)	protein.degradation.aspartate protease	-2.18	6.47E-05	-1.37	3.98E-06
solyc01g101240.2.1	3	Aspartic proteinase	protein.degradation.aspartate protease	-1	9.74E-05	0.87	6.13E-04
solyc12g042060.1.1	3	ATP-dependent clp protease ATP-binding subunit	protein.degradation.serine protease	-1.48	1.90E-02	-0.24	ns
solyc10g049710.1.1	3	ATP-dependent Clp protease proteolytic subunit	protein.degradation.serine protease	-0.73	2.90E-03	0.09	ns
solyc01g105410.2.1	3	Os06g0220000 protein (Fragment)	signalling.in sugar and nutrient physiology	-0.37	ns	-1.24	9.46E-04
solyc03g118510.2.1	3	Receptor like kinase. RLK	signalling.receptor kinases.leucine rich repeat III	-1.05	8.63E-05	-0.44	2.03E-04
solyc11g056680.1.1	3	LRR receptor-like serine	signalling.receptor kinases.leucine rich repeat XI	-1.32	5.25E-05	0.78	1.20E-02
solyc02g064940.1.1	3	LRR receptor-like serine	signalling.receptor kinases.leucine rich repeat XI	-0.92	3.16E-06	-0.49	1.84E-03
solyc04g012120.2.1	3	14-3-3 protein beta	signalling.14-3-3 proteins	-1.17	5.14E-05	-0.2	ns
solyc08g006890.2.1	3	Tubulin alpha-3 chain	cell.organisation	-1.68	7.56E-04	-0.01	ns
solyc11g010560.1.1	3	Kinesin-like protein	cell.organisation	-1.02	1.16E-04	-0.41	7.76E-04
solyc08g066110.2.1	3	Profilin	cell.organisation	-0.68	1.51E-04	0.48	3.85E-03

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Table A.3. (cont.)

ID	Cluster	Description	MAPMAN Category	*SARK::IPTs/ SARK::IPTc*	Pval_SARK::IPT	MMs/ MMc	Pval_MM
solyc10g086760.1.1	3	Tubulin beta chain	cell.organisation	-1.45	1.70E-03	0.67	2.01E-01
solyc10g080500.1.1	3	Actin	cell.organisation	-1.15	8.11E-06	-0.36	ns
solyc09g009430.2.1	3	Cell division protein ftsZ	cell.division	-0.66	2.46E-05	-0.31	ns
solyc01g007150.2.1	3	Coatomer subunit beta-1	cell.vesicle transport	-0.81	2.86E-04	0.14	ns
solyc02g079770.2.1	3	DAG protein	development.unspecified	-0.71	8.45E-03	0	ns
solyc07g017780.2.1	3	H-ATPase	transport.p- and v-ATPases	-1.35	4.26E-04	-0.38	ns
solyc06g071100.2.1	3	H-ATPase	transport.p- and v-ATPases	-1.44	1.25E-03	-0.28	ns
solyc12g056220.1.1	3	Aquaporin	transport.Major Intrinsic Proteins.PIP	-0.51	8.48E-05	-1.06	1.80E-03
solyc06g064940.2.1	3	Phosphatidylinositol transfer protein SFH5	transport.misc	-0.73	4.70E-05	-0.44	4.71E-02
solyc05g013850.2.1	3	Sieve element-occluding protein 3	not assigned.unknown	-1.14	2.57E-05	-0.08	ns
solyc06g071050.2.1	3	Spfh domain	not assigned.unknown	-1.04	1.18E-04	-0.19	ns
solyc12g095760.1.1	3	Diphosphate--fructose-6-phosphate 1-phosphotransferase	not assigned.unknown	-0.85	1.26E-02	0.66	1.35E-04
solyc06g007760.2.1	3	Ycf54 protein	not assigned.unknown	-0.78	1.62E-05	-0.64	1.83E-05
solyc06g069030.2.1	3	PAP fibrillin domain containing protein expressed	not assigned.unknown	-0.55	2.91E-03	-0.77	6.61E-06
solyc06g068220.2.1	3	Hydrolase alpha	not assigned.unknown	-1.1	1.16E-03	-0.93	8.00E-08
solyc01g010640.2.1	3	Uncharacterized membrane protein	not assigned.unknown	-0.38	ns	-0.52	2.20E-02
solyc08g067030.2.1	3	Os01g0611000 protein (Fragment)	not assigned.unknown	-2.03	1.20E-07	-0.79	3.20E-04
solyc03g111810.2.1	3	Sieve element-occluding protein 3	not assigned.unknown	-1.47	3.58E-05	-0.23	ns
solyc03g113220.2.1	3	SPFH domain	not assigned.unknown	-0.17	ns	-0.55	5.17E-04
solyc03g115020.2.1	3	Unknown Protein	not assigned.unknown	-0.74	3.88E-03	-0.71	1.20E-03
solyc07g055060.2.1	3	Phosphoenolpyruvate carboxylase 1	not assigned.unknown	-1.08	3.12E-04	0.04	ns
solyc07g006650.2.1	4	Xylose isomerase	minor CHO metabolism.others.Xylose isomerase	-0.68	4.36E-03	0.88	1.73E-03
solyc06g053200.2.1	4	6-phosphogluconolactonase	OPP.oxidative PP.6-phosphogluconolactonase	-0.22	ns	0.99	2.80E-07

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Table A.3. (cont.)

ID	Cluster	Description	MAPMAN Category	*SARK::IPTs/ SARK::IPTc*	Pval_SARK::IPT	MMs/ MMc	Pval_MM
solyc11g044910.1.1	4	Beta-xylosidase 1	cell wall.degradation.mannan-xylose-arabinose-fucose	0.26	ns	0.42	8.54E-04
solyc06g071000.2.1	4	N-succinylglutamate 5-semialdehyde dehydrogenase	amino acid metabolism.degradation.glutamate family.proline	0.67	1.86E-03	1.51	1.00E-08
solyc06g050980.2.1	4	Ferritin	metal handling.binding, chelation and storage	0.42	6.13E-04	0.9	3.50E-07
solyc04g056390.2.1	4	Isopentenyl-diphosphate delta-isomerase	secondary metabolism.isoprenoids.mevalonate pathway.isopentenyl pyrophosphate:dimethyllallyl pyrophosphate isomerase	0.45	ns	0.77	7.93E-04
solyc06g060800.2.1	4	Gibberellin 2-beta-dioxygenase	hormone metabolism.ethylene.synthesis-degradation	-0.54	3.42E-03	0.77	4.18E-03
solyc02g036350.2.1	4	1-aminocyclopropane-1-carboxylate oxidase	hormone metabolism.ethylene.synthesis-degradation	0.95	1.14E-05	1.51	1.00E-08
solyc02g082920.2.1	4	Endochitinase (Chitinase)	stress.biotic	1.07	6.93E-05	0.99	1.44E-03
solyc01g059930.2.1	4	Universal stress protein	stress.abiotic.cold	-0.15	ns	0.77	3.26E-05
solyc08g023440.2.1	4	Early-responsive to dehydration 4	stress.abiotic.drought/salt	0.31	ns	1.41	1.94E-04
solyc05g054760.2.1	4	Dehydroascorbate reductase (Fragment)	redox.ascorbate and glutathione.ascorbate	0.94	8.07E-04	0.77	4.01E-04
solyc01g067740.2.1	4	Superoxide dismutase	redox.dismutases and catalases	1.23	8.16E-04	2.53	4.94E-06
solyc03g097910.2.1	4	Dihydroorotate dehydrogenase family protein	nucleotide metabolism.degradation.pyrimidine.dihydrouracil dehydrogenase	0.19	ns	1.1	4.00E-08
solyc03g122180.2.1	4	mRNA 3-UTR binding protein	RNA.RNA binding	0.01	ns	0.6	6.07E-05
solyc04g009540.1.1	4	50S ribosomal protein L10	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.50S subunit.L10	0.02	ns	0.67	7.57E-03
solyc12g014390.1.1	4	50S ribosomal protein L13	protein.synthesis.ribosomal protein.prokaryotic.chloroplast.50S subunit.L13	-0.59	3.69E-04	0.64	3.02E-04
solyc01g096590.2.1	4	30S ribosomal protein S10	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S20	-0.4	4.07E-03	0.65	3.16E-04
solyc06g064470.2.1	4	Ribosomal protein L7a	protein.synthesis.ribosomal protein.eukaryotic.60S subunit.L7A	-0.24	ns	0.79	3.26E-04
solyc07g041900.2.1	4	Cathepsin L-like cysteine proteinase	protein.degradation.cysteine protease	0.86	1.58E-04	1.69	9.00E-11

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Table A.3. (cont.)

ID	Cluster	Description	MAPMAN Category	*SARK::IPTs/ SARK::IPTc*	Pval_SARK::IPT	MMs/ MMc	Pval_MM
solyc12g088670.1.1	4	Cathepsin B-like cysteine proteinase	protein.degradation.cysteine protease	-0.23	ns	0.53	1.08E-03
solyc01g106820.2.1	4	Peptidase M50 family	protein.degradation.metalloprotease	0.35	ns	1.12	2.72E-05
solyc07g008800.2.1	4	chaperonin	protein.folding	0.67	1.86E-04	0.52	2.98E-06
solyc02g081170.2.1	4	Plastid-lipid-associated protein. chloroplastic	cell.organisation	0.87	2.62E-04	1.13	1.00E-08
solyc04g073990.2.1	4	Annexin	cell.organisation	0.52	6.45E-03	1.65	6.60E-04
solyc06g076970.2.1	4	Peptidyl-prolyl cis-trans isomerase	cell.cycle.peptidylprolyl isomerase	-0.09	ns	0.71	1.51E-06
solyc01g095150.2.1	4	Late embryogenesis abundant protein (Fragment)	development.late embryogenesis abundant	0.11	ns	1.74	3.50E-07
solyc09g018750.2.1	4	Inosine-5	not assigned.unknown	0.67	7.43E-04	0.43	2.80E-04
solyc01g021670.2.1	4	POT family domain containing protein expressed	not assigned.unknown	-0.41	ns	0.9	1.39E-03
solyc06g076480.2.1	4	Pentapeptide repeat-containing protein	not assigned.unknown	0.02	ns	1.25	2.07E-03
solyc03g082890.2.1	4	Pentapeptide repeat protein	not assigned.unknown	0.32	ns	0.22	ns
solyc08g074620.1.1	4	Polyphenol oxidase	not assigned.unknown	1.45	7.60E-07	1.58	4.02E-04
solyc01g108910.2.1	4	COSII	not assigned.unknown	0.77	3.39E-03	2.84	1.00E-09

Table A. 4. List of proteins differentially regulated in transgenic and nontransgenic plants grown under drought stress condition from leaf nuclear enriched protein extract.

ID	Cluster	Description	MAPMAN Category	*SARK::IPTs/ SARK::IPTc*	Pval_SARK::IPT	MMs/ MMc	Pval_MM
solyc01g014210.1.1	1	ADP ATP carrier protein-like	major CHO metabolism.synthesis.starch.transporter	0.11	ns	-0.68	5.32E-03
solyc04g007070.2.1	1	Cc-nbs-lrr, resistance protein	stress.biotic	0.01	ns	-0.61	1.05E-05
solyc01g100320.2.1	1	Thioredoxin_protein disulfide isomerase	redox.thioredoxin	0.9	1.24E-02	-0.49	1.73E-02
solyc09g075200.2.1	1	U small nuclear ribonucleoprotein A	RNA.processing.splicing	-0.01	ns	-0.76	4.22E-02
solyc01g009090.2.1	1	Serrate RNA effector molecule homolog	RNA.regulation of transcription.C2H2 zinc finger family	0.59	6.83E-03	-0.48	5.41E-03
solyc02g068100.2.1	1	SWI_SNF related matrix associated actin dependent regulator of chromatin subfamily d member	RNA.regulation of transcription.Chromatin Remodeling Factors	0.62	3.01E-03	-0.55	1.54E-02
solyc03g118020.2.1	1	Tudor _ nuclease domain-containing protein	RNA.regulation of transcription.Zn-finger(CCHC)	0.52	8.32E-04	-0.37	ns
solyc03g111840.2.1	1	Polyadenylate-binding protein -like	RNA.RNA binding	0.94	2.73E-05	-0.4	2.84E-04
solyc11g011130.1.1	1	THO complex subunit 4	RNA.RNA binding	0.08	ns	-0.71	2.11E-02
solyc04g014460.2.1	1	RNA binding protein	RNA.RNA binding	0.81	1.31E-02	-0.73	4.35E-03
solyc01g006940.2.1	1	Poly(U)-binding-splicing factor PUF60	RNA.RNA binding	0.64	6.37E-04	-0.51	1.98E-02
solyc09g090960.2.1	1	RNA-binding protein	RNA.RNA binding	1.04	1.00E-08	-0.92	3.52E-03
solyc01g097010.2.1	1	Nucleic acid binding protein	RNA.RNA binding	0.7	2.42E-04	-0.42	ns
solyc11g045180.1.1	1	ATP-dependent RNA helicase	DNA.synthesis/chromatin structure	0.86	1.95E-02	-0.89	8.94E-03
solyc04g005020.2.1	1	WD-40 repeat family protein	DNA.synthesis/chromatin structure	0.64	8.54E-05	-0.18	ns
solyc03g097370.2.1	1	DNA helicase-like	DNA.unspecified	0.14	ns	-0.96	1.24E-03
solyc10g081030.1.1	1	Nascent polypeptide-associated complex alpha subunit-like protein	protein.synthesis.elongation	0.97	7.84E-03	-0.56	3.33E-02
solyc06g052030.2.1	1	Importin subunit beta	protein.targeting.nucleus	0.01	ns	-0.54	2.26E-03
solyc03g007670.2.1	1	SGT	protein.postranslational modification	0.32	ns	-0.89	ns
solyc05g009600.2.1	1	Phosphatase 2A regulatory A subunit	protein.postranslational modification	0.96	3.25E-02	-0.92	2.54E-03
solyc01g099110.2.1	1	Xaa-pro aminopeptidase	protein.degradation	0.81	1.43E-02	-1	1.19E-02

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Table A.4. (cont.)

ID	Cluster	Description	MAPMAN Category	*SARK::IPTs/ SARK::IPTc*	Pval_SARK::IPT	MMs/ MMc	Pval_MM
solyc09g011450.2.1	1	cDNA clone J075093E0 full insert sequence	protein.degradation.ubiquitin.proteasom	0.56	1.45E-02	-0.74	1.52E-03
solyc09g082320.2.1	1	Proteasome subunit beta type	protein.degradation.ubiquitin.proteasom	0.96	1.21E-04	-0.28	ns
solyc11g008500.1.1	1	Actin	cell.organisation	0.64	9.36E-03	-0.89	2.07E-03
solyc08g015690.2.1	1	Late-embryogenesis abundant protein 2	development.late embryogenesis abundant	0.81	ns	-0.54	ns
solyc05g006170.2.1	1	NACHT, LRR and PYD domains-containing protein 5	development.unspecified	0.47	ns	-1.29	4.40E-02
solyc07g066030.2.1	1	Proteasome activator subunit 4-like	not assigned.unknown	0.42	4.12E-04	-0.56	1.80E-04
solyc01g009080.2.1	1	FHA domain containing protein	not assigned.unknown	1.03	2.06E-04	-1.08	5.40E-06
solyc01g099770.2.1	1	Translationally-controlled tumor protein homolog	not assigned.unknown	0.78	5.21E-04	-0.95	7.31E-05
solyc09g013100.2.1	1	RNA binding protein	not assigned.unknown	0.65	4.10E-03	-0.24	ns
solyc04g008520.2.1	1	Outer envelope protein	not assigned.unknown	0.41	ns	-1.33	2.11E-02
solyc02g089260.2.1	2	E3 ubiquitin-protein ligase UBR4	hormone metabolism.auxin.signal transduction	0.78	6.00E-07	0.2	ns
solyc06g076520.1.1	2	class I heat shock protein	stress.abiotic.heat	0.69	9.00E-07	0.87	4.52E-04
solyc12g043110.1.1	2	Heat shock protein 4	stress.abiotic.heat	0.55	9.54E-04	0.15	ns
solyc08g080580.2.1	2	Myb	RNA.regulation of transcription.MYB domain transcription factor family	0.64	6.51E-03	0.52	1.05E-02
solyc05g007100.2.1	2	DNA-binding protein p24	RNA.regulation of transcription.putative transcription regulator	0.61	2.34E-03	0.27	ns
solyc01g049680.2.1	2	Transcriptional activator protein Pur-alpha	RNA.regulation of transcription.unclassified	1.21	5.12E-03	-0.04	ns
solyc09g090520.2.1	2	Heterogeneous nuclear ribonucleoprotein A3	RNA.RNA binding	0.95	8.72E-03	0.4	ns
solyc02g084240.2.1	2	H histone-like protein	DNA.synthesis/chromatin structure.histone	1.64	2.63E-05	0.4	8.27E-04
solyc03g117780.2.1	2	UV excision repair protein RAD23	DNA.repair	1.01	1.91E-02	1.44	1.04E-04
solyc01g066840.2.1	2	40S ribosomal protein S2	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S21	0.23	ns	0.85	6.72E-05
solyc10g078630.1.1	2	40S ribosomal protein S28	protein.synthesis.ribosomal protein.eukaryotic.40S subunit.S28	0.64	2.26E-03	-0.09	ns

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Table A.4. (cont.)

ID	Cluster	Description	MAPMAN Category	*SARK::IPTs/ SARK::IPTc*	Pval_SARK::IPT	MMs/ MMc	Pval_MM
solyc04g009410.2.1	2	Penescence-associated protein DIN	protein.degradation.ubiquitin.proteasom	1.33	5.14E-05	0.08	ns
solyc01g091460.2.1	2	ARF guanine-nucleotide exchange factor 2	signalling.G-proteins	0.83	8.10E-06	0	ns
solyc06g062350.2.1	2	Holliday junction ATP-dependent DNA helicase ruvB	development.unspecified	1.11	3.20E-08	-0.01	ns
solyc03g121500.2.1	2	Myosin-like protein	not assigned.unknown	0.64	1.80E-05	0.73	7.74E-05
solyc06g008150.2.1	2	Ulp peptidase-like	not assigned.unknown	1.05	1.67E-04	0.89	1.32E-02
solyc09g092380.2.1	2	Adenosylhomocysteinase	not assigned.unknown	0.75	3.20E-06	0.11	ns
solyc04g054880.2.1	2	BZIP transcription factor	not assigned.unknown	0.77	1.10E-06	-0.01	ns
solyc11g068640.1.1	2	Osg075900 protein (Fragment)	not assigned.unknown	1.06	8.02E-05	0.09	ns
solyc04g082200.2.1	2	Dehydrin	not assigned.unknown	2.64	1.26E-04	0.38	ns
solyc12g015880.1.1	3	Heat shock protein 90	stress.abiotic.heat	-0.72	4.00E-07	-0.26	ns
solyc01g014850.2.1	3	Zinc finger CCCH domain-containing protein 4	RNA.regulation of transcription.C3H zinc finger family	-0.4	6.98E-03	0.32	ns
solyc03g123530.2.1	3	CCAAT-box-binding transcription factor-like protein	RNA.regulation of transcription.CCAAT box binding factor family, DR1	-0.85	2.13E-02	1.05	3.18E-04
solyc01g007070.2.1	3	BEL-like homeodomain protein	RNA.regulation of transcription.HB,Homeobox transcription factor family	-0.79	ns	0.76	9.41E-03
solyc02g014770.2.1	3	Chromodomain-helicase-DNA-binding protein 6	RNA.regulation of transcription.Chromatin Remodeling Factors	-1.05	2.63E-04	0.07	ns
solyc09g009030.2.1	3	Histone deacetylase 2a-like	RNA.regulation of transcription.HDA	-1.33	8.80E-06	0.09	ns
solyc02g067210.2.1	3	Nucleic acid binding protein	RNA.RNA binding	-0.72	2.90E-04	-0.31	2.73E-04
solyc04g074040.2.1	3	RNA-binding protein	RNA.RNA binding	-1.35	8.98E-04	-0.37	ns
solyc12g014210.1.1	3	RNA binding protein	RNA.RNA binding	-0.8	7.12E-04	0.79	ns
solyc02g081810.2.1	3	tRNA pseudouridine synthase B	DNA.synthesis/chromatin structure	-1.99	1.00E-08	-0.28	ns
solyc02g064700.2.1	3	Protein serine_threonine kinase	protein.postranslational modification	-0.75	2.44E-04	0	ns
solyc03g082960.2.1	3	Serine_threonine phosphatase family protein	protein.postranslational modification	-0.65	6.54E-03	0.63	ns

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Table A.4. (cont.)

ID	Cluster	Description	MAPMAN Category	*SARK::IPTs/ SARK::IPTc*	Pval_SARK::IPT	MMs/ MMc	Pval_MM
solyc02g081010.1.1	3	Transcription factor jumonji domain-containing protein	protein.degradation.ubiquitin.E3.RING	-0.71	1.25E-03	0.00E+00	ns
solyc04g051370.2.1	3	26S proteasome non-ATPase regulatory subunit 2	protein.degradation.ubiquitin.proteasom	-0.65	7.16E-03	-0.23	ns
solyc00g323130.2.1	4	Major latex-like protein	stress.abiotic.unspecified	-0.5	7.00E-07	-0.72	1.74E-02
solyc01g107870.2.1	4	Poly(A) RNA binding protein	RNA.processing	-1.11	1.10E-06	-1.58	3.04E-05
solyc11g072340.1.1	4	Arginine_serine-rich splicing factor	RNA.processing.splicing	-0.31	ns	-0.84	1.61E-02
solyc01g107330.2.1	4	SWIB_MDM2 domain protein	RNA.regulation of transcription.Chromatin Remodeling Factors	0.08	ns	-1.75	4.73E-02
solyc07g052900.1.1	4	Os09g045700 protein (Fragment)	RNA.regulation of transcription.GeBP like	-0.04	ns	-1.98	4.14E-03
solyc03g114370.2.1	4	Atp-dependent RNA helicase	DNA.synthesis/chromatin structure	-1	2.41E-03	-1.61	1.04E-02
solyc02g087400.1.1	4	Ankyrin repeat domain containing protein	DNA.synthesis/chromatin structure	-0.3	ns	-1.12	3.40E-03
solyc02g091960.2.1	4	Nuclear matrix constituent protein 2	protein.degradation	-0.19	ns	-0.73	8.14E-04
solyc04g071320.2.1	4	Protein FAM88A	protein.degradation.ubiquitin	0.15	ns	-2.28	1.60E-03
solyc06g063140.2.1	4	26S protease regulatory subunit 7	protein.degradation.ubiquitin.proteasom	-0.18	ns	-1.09	2.17E-04
solyc10g006330.2.1	4	Unknown Protein	cell.organisation	-0.6	1.72E-02	-1.28	1.54E-03
solyc07g047670.2.1	4	Pescadillo homolog	development.unspecified	-0.8	7.49E-03	-1.15	3.94E-05

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Publications

Şelale, Hatice, Fatih Dağlı, Nedim Mutlu, Sami Doğanlar, and Anne Frary. "Cry1Ac-mediated resistance to tomato leaf miner (Tuta absoluta) in tomato." *Plant Cell, Tissue and Organ Culture (PCTOC)* 131, no. 1 (2017): 65-73.

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