SYSTEMIN INVOLVEMENT IN TOMATO DEFENSE PRIMING

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RIASSUNTO

Le piante sono organismi sessili incapaci di sfuggire alle variazioni sfavorevoli dell'ambiente. Per contrastare tale condizione, questi organismi hanno evoluto meccanismi elaborati per percepire lo stress e adattarsi ad esso attraverso alterazioni rapide, dinamiche e complesse.
Le difese delle piante possono essere distinte in base al tempo di attivazione, in difese costitutive, sempre espresse, e difese inducibili se espresse dopo attacco dei parassiti. Sulla base del meccanismo d'azione, le difese della pianta possono essere distinte in dirette e indirette: le prime interferiscono direttamente con la crescita e lo sviluppo degli insetti, le altre sono attive nel reclutamento dei nemici naturali degli insetti. Sono incluse nelle difese dirette le barriere fisiche quali spine, silice, tricomi, che rendono difficoltosa la colonizzazione da parte dei parassiti, metaboliti primari o secondari come inibitori di proteasi e polifenolo ossidasi che determinano una diminuzione dei livelli di digestione e dell'assimilazione dei nutrienti, compromettendo la crescita degli insetti, ma anche composti tossici come alcaloidi, terpenoidi e fenoli che interferiscono con il metabolismo dell'insetto (Bennet e Wallsgrove, 1994; Kessler e Baldwin, 2002; Campbell et al., 2013).
Le difese indirette includono la produzione di composti organici volatili (VOCs), coinvolti nell'attrazione di nemici naturali dei degli insetti, come i predatori e i parassitoidi (Dudareva et al. 2006). I VOCs includono inoltre semiochimici coinvolti nella segnalazione aerea inter-pianta e pianta-pianta. E' noto, infatti che i VOCs possono segnalare 'pericolo di attacco' da parte di erbivori o altri parassiti. e possono segnalare pericolo di attacco da parte di erbivori. Le piante allertate sono in uno "stato innescato", ossia più rapide ed efficienti nell'induzione delle difese a seguito di attacco di erbivori (Hilker e Meiners, 2009). Quindi, l'esposizione ai composti organici volatili prodotti da piante attaccate da erbivori può innescare nella pianta esposta non ancora danneggiata meccanismi molecolari che la preparano ad una risposta difensiva, incrementando così la probabilità di sopravvivenza ad un attacco. Tale fenomeno è denominato "Priming", di cui sono ancora ancora poco noti i meccanismi molecolari che lo sottendono.
Nelle *Solanaceae*, le sistemine sono una famiglia di peptidi coinvolti nell'attivazione di geni di difesa in risposta a ferite e agli attacchi di erbivori masticatori (Ryan e Pearce, 2003).
La Sistemina (Sys) è un ormone peptidico di 18 amminoacidi, rilasciato inizialmente dai siti di danno e rappresenta un segnale primario di ferita in pomodoro. La Sistemina è rilasciata da una proteina precursore, citosolica, di 200 aminoacidi chiamata ProSistemina (ProSys) mediante un meccanismo ancora non noto. L'attivazione di geni di difesa mediata da Sistemina avviene attraverso la via degli octadecanoidi, i cui prodotti sono acido jasmonico (JA) e suoi derivati. Dopo l'attacco da parte di erbivori, la Sistemina viene rilasciata dal suo precursore e potrebbe legarsi ad un recettore non ancora identificato attivando un complesso percorso di segnalazione intracellulare con conseguente attivazione di proteine chinasi mitogeno-attivate (MAPK), la rapida alcalinizzazione del mezzo extracellulare, l'attivazione della fosfolipasi A2 e il rilascio di acido linolenico dalle membrane con conseguente innesco del pathway degli octadecanoidi.
Recenti studi hanno evidenziato il coinvolgimento della Sistemina nella promozione di difese del pomodoro ad ampio spettro, contro diverse tipologie di stress (Orsini et al., 2010; Coppola et al., 2014). Un precedente studio ha mostrato che l'espressione costitutiva di ProSys in piante di pomodoro induce la modifica della miscela di VOCs

sia a livello quantitativo che qualitativo, rendendo le piante transgeniche più attrattive nei confronti di *Aphidius ervi*, un parassitoide dell'afide (Corrado et al., 2007). Le emergenti evidenze sul *priming* delle difese endogene della pianta e le osservazioni sull'azione della Sistemina nella difesa del pomodoro, hanno motivato uno studio che mira a valutare l'effetto di questo ormone sul *priming* delle difese mediante segnalazioni aeree volatili. Questo obiettivo si inserisce nel contesto della promozione delle naturali difese delle piante, per l'ottimizzazione di sistemi integrati di controllo degli insetti erbivori.

La valutazione dell'effetto della Sistemina nel *priming* delle difese di piante di pomodoro è stata effettuata mediante l'esposizione di piante sane a tre diversi tipi di piante sorgenti:

1- Piante masticate da larve di *Spodoptera littoralis* (S1)
2- Piante esprimenti in maniera costitutiva il cDNA codificante per la ProSistemina (S2)
3- Piante con applicazioni fogliari del peptide di sintesi Sistemina (S3).

Pertanto, gli obiettivi dell'attività di tesi sono consistiti innanzitutto nella valutazione della funzionalità del peptide e nella valutazione del suo effetto nelle comunicazioni pianta-pianta. L'attività biologica del peptide è stata effettuata in base alla sua capacità di indurre geni correlati con la difesa, a confronto con piante attaccate da larve di lepidottero, nelle quali il ruolo della Sistemina è stato ampiamente descritto (Ryan, 2000; Conrath, 2009; Walling, 2009; Kessler e Baldwin, 2002; Howe, 2004) e con piante transgeniche sovra-esprimenti il gene del precursore della Sistemina, la ProSistemina.

Un'analisi di espressione in time-course del gene ProSys e di quello codificante per l'inibitore di proteasi I (*InhI*) in seguito a masticazione di *S. littoralis* ha permesso di evidenziare quale fosse il tempo ottimale per avere una massima influenza del danno nella trasduzione del segnale mediata dalla Sistemina. Per questa analisi larve di *S. littoralis* sono state alimentate su piante "Red Setter" per 1 ora. I risultati hanno evidenziato che la masticazione induce, come atteso, la trascrizione del gene *ProSys* che risulta indotto esclusivamente al sito di danno in tempi, in perfetta concordanza con il suo ruolo di segnale precoce. Il valore massimo di RQ raggiunto da questo gene è di 4 volte, una induzione piuttosto debole tipica delle molecole segnale che hanno la capacità di attivare cascate di difesa a valle (Howe e Jander, 2008), mentre il gene *InhI*, invece, responsabile dell'attività antidigestiva che si esplicita nell'intestino dell'insetto, è espresso sia nelle foglie locali che distali raggiungendo livelli di induzione elevatissimi. Anche *LoxC* e *AOS*, geni precoci coinvolti nella conversione dell'acido linoleico in acido jasmonico (Ryan, 2000) mostrano un attivazione simile.

Studi recenti hanno confermato che piante sovraesprimenti il gene della ProSistemina sono in grado di difendersi da numerosi stress biotici, attivando una vasta gamma di segnali difensivi ce inducono tolleranza all'attacco di funghi necrotrofici e di afidi (Coppola et al., 2014). Inoltre, l'overespressione della ProSistemina promuove la produzione di una miscela di volatili maggiormente attrattive verso ii parassitoide *Aphidius ervi* (Corrado et al., 2007). Alla base di questa maggiore tolleranza agli attacchi e della promozione delle difese, le piante transgeniche hanno mostrato una riprogrammazione del trascrittoma che coinvolge numerosi pathways difensivi (Coppola et al., 2014). Tali osservazioni hanno giustificato la scelta di queste piante come un sistema sorgente di composti volatili in una condizione che mima un costante attacco, o meglio, difese sempre attivate.

Per valutare l'attività del peptide somministrato dall'esterno e capire se riuscisse a riprodurre gli effetti della Sistemina nei meccanismi di difesa in pianta, sono state applicate sulle foglie diverse concentrazioni di peptide e poi è stata eseguita un'analisi dei geni espressi strettamente correlati al peptide stesso, il gene *ProSys*, codificante per il suo precursore, e il gene *InhI*, codificante per un inibitore di proteasi attivato dallo stimolo indotto dalla Sistemina (Ryan, 2000). Applicazioni picomolari di peptide inducono l'espressione della ProSistemina, mentre anche concentrazioni fM del peptide attivano il gene *InhI* già 6 ore dopo la sua applicazione. E' possibile quindi che il peptide Sys sia internalizzato probabilmente mediante endocitosi mediata da un recettore.
Stabilita l'adeguatezza delle piante sorgenti selezionate, lo studio è stato focalizzato sull'individuazione delle opportune condizioni sperimentali idonee per l'induzione del *defense priming*. A tale scopo, è stata allestita l'esposizione di piante di pomodoro sane (riceventi), allevate in piccoli box isolati, alle tre tipologie di sorgenti precedentemente menzionate e verificato ll'effetto dell'esposizione attraverso il monitoraggio dell'espressione di un gruppo di geni correlati con la difesa: *GCS*, germacrene-C-syntase, coinvolto nella sintesi di terpenoidi (Colby et al., 1998; Falara et al., 2011); *InhI* e *InhII*, inibitori di proteasi attivati in seguito a fitofagia (McGurl et al., 1994); *LoxA*, *LoxC* e *LoxD*, lipossigenasi coinvolte nei primi step della biosintesi dell'acido jasmonico (Ryan, 2000; Feussner e Wasternack, 2002; Li et al., 2002); *MPK1*, una chinasi coinvolta nella trasduzione del segnale di difesa (Walling, 2009); *WRKY40*, un fattore trascrizionale coinvolto in numerose risposte a stress biotici e abiotici (Dicke e Baldwin, 2010).
Gli esperimenti sono stati effettuati in un sistema chiuso esponendo piante Riceventi alle rispettive Sorgenti in un rapporto 1:1. Sono state raccolte le foglie dalle piante riceventi a diversi tempi di esposizione da cui è stato estratto RNA totale per l'analisi dell'espressione dei geni precedentemente citati. Per le tre tesi analizzate, il profilo d'espressione dei geni testati è risultato differenzialmente regolato nelle piante riceventi. Questo risultato dimostra che i segnali emessi dalle piante sorgenti sono percepiti dalle riceventi che, di conseguenza, attivano l'espressione di geni di difesa. In letteratura sono diversi i lavori che attestano che quanto osservato in questo esperimento è un meccanismo utilizzato dalle piante per comunicare diverse situazioni di pericolo o di stress (Kost e Heil, 2008; Kessler et al., 2006). Queste osservazioni e i dati di espressione prodotti indicano chiaramente che le condizioni sperimentali adottate erano idonee per lo studio del priming.
A supporto dei dati molecolari ottenuti, sono stati allestiti biosaggi volti a determinare se la modulazione di questi geni si traducesse in efficace incremento delle difese dirette e indirette contro insetti. E' stata quindi valutata la crescita ponderale e la sopravvivenza di larve di *S. littoralis* alimentate su foglie di piante riceventi esposte ai tre tipi di piante sorgenti utilizzate. I dati ottenuti mostrano che le larve alimentate su foglie di piante esposte alle sorgenti S2 e S3 hanno un ridotto incremento del peso e un tasso di mortalità più alto rispetto al controllo. Questi risultati dimostrano l'attivazione dei geni di difesa nelle piante riceventi è in grado di contrastare efficacemente l'attacco dell'insetto erbivoro. È noto che le piante sorgenti utilizzate in questo studio siano più attrattive nei confronti di parassitoidi d'insetti erbivori. Infatti, è stato visto che piante di pomodoro sovraesprimenti la ProSistemina sono più attrattive nei confronti del parassitoide dell'afide *Macrosiphon euphorbiae*, *Afidius ervi* (Corrado et al., 2007) così come piante masticate da larve di *S. littoralis* risultano maggiormente attrattive verso il terzo livello trofico (Kessler and Baldwin, 2002). Avendo stabilito che i volatili emessi dai diversi tipi di sorgenti in esame sono in

grado di attivare le difese dirette delle piante esposte, è stato indagato il possibile effetto sull'attrattività del terzo livello trofico. La possibilità che piante non attaccate esposte ai VOCs emessi in presenza di Sistemina, sia essa applicata sulle foglie o generata endogenamente, è stata valutata mediante un saggio di attrattività in *wind tunnel* nei confronti del parassitoide di afidi, *Afidius ervi*. Questo saggio permette di stabilire quanto un parassitoide preferisca e scelga una pianta piuttosto che un'altra, scelta influenzata essenzialmente dalle miscele di VOCs emesse. Ciascuna pianta ricevente esposta alla corrispondente sorgente è stata posta in galleria del vento ed è stata calcolata la percentuale dei voli orientati e gli atterraggi diretti del parassitoide. Le piante di pomodoro esposte a tutte e tre le sorgenti utilizzate hanno fatto registrato una percentuale di voli orientati e di atterraggi superiore a quelli registrati per le piante controllo.
Questi risultati hanno motivato l'analisi qualitativa e quantitativa di VOCs prodotti dalle diverse piante sorgenti e riceventi. I VOCs sono stati rilevati attraverso Gas cromatografia-Spettrometria di Massa. Questa analisi ha mostrato per le sorgenti che piante masticate e piante sovraesprimenti la ProSistemina emettono miscele di volatili qualitativamente diverse da quella del controllo, caratterizzate per lo più da terpeni e sostanze altamente odorose attrattive nei confronti dei predatori dei parassiti della pianta (Kessler and Baldwin, 2002). Inoltre, i risultati ottenuti hanno dimostrato che la somministrazione fogliare del peptide modifica la miscela di composti di volatili emessi dalla pianta trattata e dalle piante riceventi. Le evidenze raccolte hanno motivato un'indagine più approfondita sulla riprogrammazione del trascrittoma delle piante esposte alla sorgente S3. La scelta di questo approfondimento si basa sul recente e crescente interesse verso l'uso di peptidi naturali per la promozione delle difese, in sistemi di controllo integrato. A tale scopo, è stato effettuato il sequenziamento del trascrittoma (RNAseq) di piante di pomodoro esposte ai VOCs emessi da piante trattate con Sistemina a livello fogliare. Foglie giovani di piante esposte sono state utilizzate per l'estrazione dell'RNA totale per il sequenziamento *paired-end* (2x100b), su piattaforma Illumina HiSeq1500. L' analisi dei dati provenienti dal sequenziamento del trascrittoma è stata condotta durante il mio soggiorno presso la Sequentia Biotech SL. (Barcellona, Spagna) ed include, la mappatura delle *reads* sul genoma di riferimento del pomodoro, e l'analisi dei valori di *fold change* per ciascuna sequenza. La riprogrammazione del trascrittoma è stata piuttosto vasta, interessando l'espressione di 1118 geni, di cui 527 sovraespressi e 581 sottoespressi. L'analisi trascrittomica spiega parte delle osservazioni biologiche effettuate dal momento che risultano differenzialmente espressi numerosi geni coinvolti nella modulazione delle difese del pomodoro e attivi in diverse vie metaboliche, come ad esempio quella che porta alla sintesi dell'acido jasmonico, potente attivatore delle difese della pianta. Geni molto precoci nella risposta, quali perossidasi, calmodulina e chinasi, associati alle specie reattive dell'ossigeno (ROS) e ai primi segnali di difesa contro insetti e funghi necrotrofi, risultano up-regolati. Tra i geni down-regolati si registrano, ad esempio, osmotine e chitinasi, geni solitamente salicilato-dipendenti, down-regolati probabilmente in conseguenza del noto antagonismo tra acido jasmonico e acido salicilico (Walling, 2000). Il lavoro svolto ha dimostrato che l'applicazione fogliare della Sistemina, incrementa le difese dirette e indirette non solo delle piante direttamente sottoposte a trattamento, ma anche nelle piante esposte alle piante trattate che risultato resistenti ad attacchi successivi di insetti erbivori. Il peptide Sistemina si propone come un nuovo agente efficace per la protezione del pomodoro, rappresentando una potenziale valida alternativa all'utilizzo di agrochimici o un valido strumento per la loro riduzione in sistemi di controllo

integrato degli insetti. Questi possibili usi richiederanno valutazioni di stabilità e di efficacia in pieno campo, oltre che l'individuazione di opportune strategie di *delivery.*

SUMMARY

As sessile organisms, plants cannot escape stress conditions so they are obliged to develop fine and elaborated defense strategies to protect themselves against different threats. Plants defend themselves against biotic and abiotic stresses via both constitutive and inducible defenses. Based on the mode of action, plant resistance traits can be distinguished in direct and indirect defenses. Volatile organic compounds (VOCs) that are released in large amount in response to herbivory and wounding, play an important role in indirect defense by the attractiveness towards natural enemies of insect pests. VOCs are also involved in a plant-to-plant communication mechanism called "*priming*" in which neighbouring plants (receivers) to infested plants (emitters), can activate their own defenses (primed state) (Conrath, 2011). In the *Solanaceae*, a family of defense-related peptide hormones called systemins are involved in the activation of defense genes in response to wounding and herbivore attacks (Ryan and Pearce 2003). Systemin (Sys) is a 18-amino-acid peptide hormone, which is initially released at wound sites, representing a primary wound signal in tomato. It activates defense genes involved in the octadecanoid signaling pathway, which leads to the production of jasmonates and C_6 volatile compounds involved in direct and indirect defenses (Ryan, 2000; Corrado et al., 2007; El Oirdi et al., 2011). The aim of this research activity is to shed more light on the molecular and chemical basis of plant defense priming; therefore, the project evaluated the involvement of systemin in the defense priming of tomato plants. Firstly, the research focused on the evaluation of direct defenses activation following Sys peptide foliar applications through the study of gene expression profiles. Once established its effectiveness in defense response activation, its attitude to induce priming in neighboring plants was evaluated. To these aims, the expression analysis of defense related genes has been carried out in receiver plants exposed to volatiles released by three different kinds of sources: plant chewed by *Spodoptera littoralis* (S1), transgenic plants constitutively expressing *ProSys* (S2), plants treated with peptide Sys (S3). The results of these analyses underlined a modulation various and continuous of gene expression indicating that the different VOCs blends were perceived by receiver plants which resulted modified in their defense gene expression profiles. The exposed plants were found to be more tolerant to *Spodoptera littoralis* that resulted compromised in its growth and survival rates. Moreover, plants exposed to the different VOCs sources were more attractive towards the parasitoid of aphids, *Aphidius ervi* compared to the control. In order to get a wider overview on transcriptome reprogramming following exposure to S3 plants a RNAseq was performed. A total number of 1118 differentially expressed genes was identified. Among them, 537 genes were up-regulated while 581 were down-regulated. The resulting molecular functions and genes were found to be associated with variation in gene expression related to metabolism and stress response. All together the results indicate that Sys foliar application influences tomato defenses not only of the treated plants but also in the sourrounding undamaged plants via airborne signals. These are very interesting findings which suggest a possible use of a peptide to promote crop protection with natural molecules, according to the necessity of a sustainable agriculture.

1. INTRODUCTION

1.1 Plant undergo a series of different stresses

Plants are sessile organisms unable to escape the negative changes of the environment. To contrast the adverse storage conditions in their environment, plants have evolved mechanisms to detect stress factors and adapt to them through rapid, dynamic and complex changes in their physiology.
Stressors in plants are external conditions which influence negatively growth, development and plant productivity.
The environmental stresses are among the major limiting factors on agricultural productivity. Stresses can be abiotic, such as drought or excess light, or biotic, as herbivores or pathogens. The biotic and abiotic stresses can reduce average crop yield by 65% to 87% (Gürsoy et al., 2012).
Abiotic stress factors like cold, heat and salinity have a strong impact on world agriculture. One of the most important abiotic stress agent for plants is water deprivation. A plant requires a certain amount of water for its optimal survival; flooding or drought stress can cause plant cells to swell or desiccation.
Moreover, plants have an optimal temperature range inside which they grow and get best performances. The thermal stress can be caused by high or low temperatures: too hot temperatures lead to cell desiccation and can cause proteins denaturation, losing their structure that is required for their biological activity. When plants grow in soils they can absorb heavy metals which may interfere with basic physiological and biochemical activities such as photosynthesis (Prasad and Strzałka, 2013).
One of the complex changes in the plant induced by abiotic stressors is the accumulation of important low-molecular compounds (sugar, polyols, amino acids) that maintain the vital functions of the cells (Slama et al., 2015).
Plants in addition to abiotic stresses have to defend themselves from several predators as they represent an easy target for many biotic stress agents such as insects, fungi, bacteria, nematodes, weeds and herbivorous animals.
Phytopatogenic fungi cause a large number of disease. Based on their lifestyle, they have been classified into necrotrophs, hemibiotrophs and biotrophs. Necrotrophic fungi are the largest group of plant fungal pathogens and cause heavy crop losses world-wide. The necrotroph *Botrytis cinerea* infects almost all vegetable and fruit crops and annually results in worldwide losses of $10 to $100 billion (Wang et al., 2014). Often, fungi manifest themselves as a secondary infection by insects. Their destroying ability is due to their ability to kill living cells before invasion taking nutrients that are released by damaged tissues. Biotrophs, instead, extracts nutrients from living cells infiltrating and establishing their *hyphae* within the cell. Hemi-biotrophic fungi combine both strategies during their life. Members of these groups include the rust fungi and powdery mildews and species in the *Ustilago*, *Cladosporium* and *Magnaporthe* genera. Among them, *Cladosporium fulvum* represents one of the most important cause of crop losses for *Solanaceae*. The disease is primarily a problem on greenhousegrown tomatoes, but can occur in the field when humidity is high. The hemibiotroph *Phytophthora infestans* is the causing agent of late blight, one of the the most important foliar fungal disease of tomato. This pathogen can spread in a very short period of time since a single lesion can produce as many as 300,000 sporangia per day (Foolad et al., 2008). The short life cycle of the disease makes the spread of infection rapid with, consequently, very huge crop losses.

Fungal diseases are often difficult to eradicate, especially in cases of massive infection and full-blown. In most cases, fungal diseases develop in conditions of excessive humidity and heat. The presence of suberin and waxes on plants slows infectious processes, but there are some fungi that synthesize cutinases, a serine esterase that hydrolyzes cutin. It was shown that secondary metabolites produced by plants have important ecological functions in plant protection against fungal infections (Bennett and Wallsgrove, 1994; Ribera and Zuniga, 2012).
Plant are also damaged by bacteria. The plant pathogenic agents are generally bacilli. The bacteria are located between a cells attacking the parenchymal tissues. Disease symptoms are represented by soft rottenness or localized necrosis. The bacteria also spread into the vascular system and the infection spreads through the raw sap. The tissues of the plant end to collapse and events appear accentuated when in bacterial infections is accompanied by the production of toxic substances (Suresh et al., 2014).
Viruses are considered the major cause of crops damage in the world (Loebenstein and Thottappilly, 2013). These agents of disease need a living cell in which multiply. Viruses always act as obligate parasites requiring the plant cell to replicate other viral entities. They are transmitted to the plants through carriers, generally represented by insects with piercing-sucking mouthparts, such as aphids. Aphids sting plant tissue to feed and, if infected, they transmit the virus. Virus infection may give rise to phenomenon of dwarfism or gigantism. Otherwise they alter leaves morphology such as curling, mosaicking, colour alterations, necrosis or symptoms charged to fruit and flowers such as glassy texture of the fruit and bronzing (Gergerich and Dolja, 2006).
Insects can cause severe physical damage to plants; plants and insects have coexisted for as long as 350 million years and have developed a series of relationships which affect the organisms at all levels, from basic biochemistry to populations genetics (Gatehouse, 2002).
Insects harmful to crops, depending on the type of mouth parts, can suck the sap (piercing-sucking insects) or remove the plant tissues (chewing insect). Many piercing-sucking insects, are extremely harmful also because they produce a sugar rich substance, honey dew which represents a nutrition source for other insects and a substrate for the development of saprophytic fungi. It is important to remember that many insects are harmful to crops only in certain stages of their life cycle, for example Lepidoptera are defoliating when they are in the larval stage.
Finally biotic stresses include weeds, considered as unwanted and unprofitable plants. The weeds have competitive action type that can be divided into direct, compete for nutrients, light, water and living space and indirect due to the release of substances into the soil that have negative effect on other plants.

1.2 Plant defenses against biotic stresses: Direct and Indirect

Based on the mode of action, plant defenses can be distinguished in direct and indirect. Direct defenses include genes and their products that interfere with nutrition, metabolism, growth and reproduction of the pests (Mithöfer and Boland, 2012). Indirect defenses involve mainly the production, in response to the attack of pests, of specific volatile organic compounds (VOCs), which are attractive to the natural enemies of the pest (Dicke and Van Loon, 2000; Heil and Ton 2008). Direct defenses are, for example, physical barriers such as thorns, silica, trichomes, or primary and secondary metabolites such as proteinase inhibitors and polyphenol oxidases that reduce digestion and nutrient assimilation impairing insects growth, and toxic

compounds such as alkaloids, terpenoids and phenolics that interfere with insect metabolism.
The plants can mediate the direct resistance in different ways:

- The antixenosis, describes a defense mechanism that produces a non-preference reaction of the pest; this occurs when there is the presence of chemical or mechanical factors that modify the behavior of the insect that can reluctantly accept or reject completely the plant as its target (Smith and Clement, 2012).
- The antibiosis occurs when the plant adversely affects the life of the pest increasing mortality or reducing the development (Smith and Clement, 2012). For example the production of inhibitors of insect digestive enzymes such as proteases and amylases, following insect attack, reduce the nutritional value of the plant material (Smith, 2010) while antinutritional proteins, such amino acids deaminases, are able to degrade amino acids necessary for pests' survival (Chen et al., 2005).

Indirect defenses are plant traits that attract predators and parasitoids of herbivores and include volatile organic compounds (VOCs) that are released in large amount in response to insect herbivory. Emission of volatile molecules from plants has been identified as an important component of the plant defense (Arimura et al., 2008). The released VOCs attract the third trophic level formed by the natural enemies of herbivorous insects (Kessler and Baldwin, 2002). In addition, some VOC compounds can also function as direct defense, for example by repelling the herbivore female ovipositing (Kessler and Baldwin, 2002).
VOCs derive from three pathways:

- The octadecanoid pathway, which produces jasmonic acid (JA) and its derivatives and Green Leaf Volatile (GLV, C_6 molecules) that derive from the degradation of C_{18} fatty acids (linolenic and linoleic acids) in C_6 and C_{12} components by hydroperoxide lyase (HPL). JA is an important hormone for induction of defense genes in plants.
- The shikimic acid pathway, which produces indolic compounds and aromatic volatiles like methyl salicylate (MeSA) which is a regulator of pathogenesis-related (PR) genes encoding proteins active against insect pests and phytopathogenic fungi.
- The terpenoids pathway, which produces a wide family of compounds involved in many biological processes including defense. There are two biosynthetic pathways, the mevalonate pathway and the non-mevalonate pathway, for the terpenoid building through isopentenyl diphosphate (IPP) and dimethylallyl diphosphate (DMAPP). From these compounds are generated geranyl diphosphate (GPP), farsenyl diphosphate (FPP) and geranylgeranyl diphosphate (GGPP), which are the precursors of monoterpenoids (C_{10}), sesquiterpenoids (C_{15}), and diterpenoids (C_{20}), respectively, all active in plant indirect defense

Many scientific evidences proved the involvement of VOCs in indirect defense. Studies conducted by Geervliet and coworkers (1994) showed that VOCs were responsible for the attraction of the enemies of chewing insects such as plant of *Brassica spp.* attacked by *Pieris brassicae* larvae that were attractive to *Cortesia rubecola* parasitoid (Geervliet et al., 1994). Other studies have shown that volatiles emitted from *Tetranychus urticae* infested lima bean plants (*Phaseolus lunatus* L.), function as signal compounds in plant-plant communication (Arimura et al., 2001). So volatiles bouquet can depend on stressed plant species or a stressor (Kask et al.,

2013) and VOCs are essential in plant-plant and plant-insect comunications (Dicke and Baldwin, 2010).
In addition, volatile blend composition is influenced by the kind of elicitors released by the insect and different plant species infested by the same herbivore show large qualitative differences of the blends emitted (Dicke, 1999). Therefore, the infested plant is able to comunicate with the third trophic level helping in the the identification of its location by the insect natural enemy, which preys the herbivore. It was also shown that the VOCs have an important role in plant-plant interaction (Farmer, 2001). VOCs including green leaf volatiles (GLV) that consist mainly of degradation products derived from C_{18} fatty acid, linolenic and linoleic acid, which, after transformation to a hydroperoxide by a lipoxygenase, are cleaved by hydroperoxide lyase (HPL) into C_{12} and C_6 components. GLVs have an important functions as airborne signal within and between plants; GLVs and VOCs releasing from resistance-expressing plants, can trigger specific defensive responses in neighboring plants (Heil and Karban, 2009).
The plants in nature emit VOCs even in conditions of normal physiological growth, but when these are attacked or damaged the volatiles quantity and quality released change (Walling, 2000). There are several factors which determine the kind of molecules in the blend of volatile, these depend mainly on the plants species, genotype involved and the stage of development (Dicke, 1999). Generally, C_6 compounds such as alcohols and aldehydes and C_{10} compounds such as terpenoids, are emitted by almost all plants species. On the countrary, specific components are species specific besides beeing also determined by insect elicitors. Several elicitor have been isolated from different plants, among them there are lytic enzymes, such as beta-glucosidase, isolated from *Pieris brassicae* that determines the release of terpenoids from leaves of cabbage (Mattiacci et al., 1995). Other important elicitors are indicated as FACs (Fatty acid-amino acid conjugates) among which the volicitin isolated from the oral secretion of *Spodoptera exigua*, and produced as a result of the formation of an amide link between the carboxyl group of linolenic acid of the the plant and the amino group of glutamine produced by the insect (Turling, 1993; Pare et al., 1998). Studies performed by Alborn and coworkers (1997) shown that the application of volicitin on injured corn plants induce the production of the same VOCs released by corn plants attacked by *Spodoptera exigua* (Alborn et al., 1997).
Overall, as previously mentioned, the VOCs involvement is crucial in both the direct and indirect defense and the strength of the emission signal can be quantitatively related to the severity of both abiotic and biotic stresses (Niinemets et al., 2013).

1.3 Time of defenses: Constitutive and Inducible responses

Plant defenses can be distinguished based on the time of their activation in constitutive defenses, always expressed, and inducible defenses if expressed after induction.
Constitutive defenses do not foresee any recognition of the pathogen: in some cases the host prevents the differentiation of the pathogen, in other cases the guest has performed physical modifications, as lignification or resin production, and chemical barriers, as deterrents of feedings or toxin, that most of the potential pathogensis notable to overcome. They include morphological features such as thorns, prickles, or high levels of lignification. Among the chemical barrier, probably the most important are the specialized metabolites of various tissues, which can be toxic, antidigestive, or unpalatable. Trichomes may full fill both features, in fact they are a

mechanical barrier, but may harbour secretory structures that contain feeding deterrents as well as toxins. The toxicity mechanisms includes inhibitor of transport or of signal transduction or of metabolism (Kessler and Baldwin 2002; Walling, 2000).
Plants inducible defenses are triggered by compounds, called elicitors, produced by the pests (Yan and Xie, 2015). These molecules can interact with specific receptor proteins located on plant cell membranes (Conrath et al., 2015). The elicitors generally have a conserved structure related with the species of insect and the type of feedings. The elicitors may also be molecules of plant origin that have undergone a change due to the attack of an insect or a pathogen, such as inceptine, present in the regurgitation of some insects upon leaves wounding (Howe and Jander, 2008) or volicitin, as previously described. Several FACs have been identified in *Manduca sexta*, the application of which to *Nicotiana attenuata* wounded leaves induces the activation of mitogen activated protein kinases (MAPK), Jasmonic Acid and Ethylene biosynthesis and signaling pathways, with the following modification of transcriptomic, proteomic, and metabolomic responses. The registered modifications are associated with the activation of direct and indirect defenses (Giri et al., 2006).
To distinguish the attacker, and in most cases identify it, plants evolved the ability to perceive herbivory associated molecular patterns (HAMPs), as activity of the plant innate immune system (Felton and Tumlinson 2008). HAMPs can be classified into two categories: (1) chemical elicitors derived from herbivore oral secretions (OS) and oviposition fluids; and (2) those that originate from the specific patterns of wounding (Wu and Baldwin, 2009). Similarly, plant may distinguish attacking pathogens though PAMPs (pathogen associated molecular patterns), microorganisms through MAMP (microbe-associated molecular pattern), and the general damage through DAMPs (damage-associated molecular pattern). The plant pattern recognition receptors specifically interact with them activating intracellular signaling, transcriptional reprogramming, and biosynthesis of metabolites that counteract the parasite growth and vitality (Conrath et al., 2015). The system is known as PAMP-Triggered Immunity (PTI) and it represents the first step of co-evolution of defence strategies described by the ZigZag model introduced by Jones and Dangl in 2006 (Figure 1).

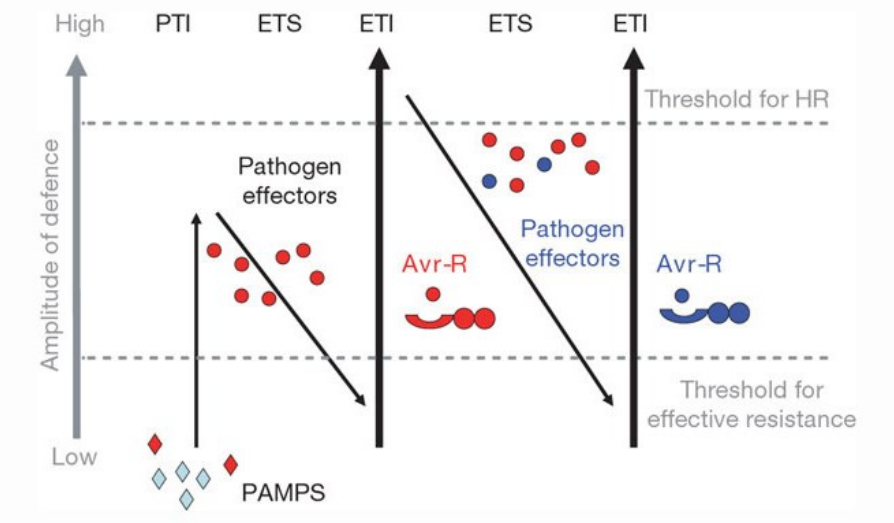


Figure 1: Zig-zag model illustrating the co-evolution between host and pathogen (Jones and Dangl, 2006).

According to Felix and Boller (2009), the plant immune system is all-inclusive: MAMPs, DAMPs, or effector, may appear to the plant as one signal that indicates a dangerous situation; in fact the gene expression data indicate that there is

considerable overlap between the defence responses induced by MAMPs, DAMPs, and other elicitors (Wise et al., 2007). In addition, observing the induced response, it appears that plants do not discriminate between the signals of danger originated from bacteria or fungi. Some pathogens have been becoming able to counteract the host's resistance baseline (PTI) injecting effectors that can promote the effector-triggered susceptibility (ETS) (Figure 1). In a subsequent phase, one of the effectors released is recognized by novel evolved plant receptors resulting in effector-triggered immunity (ETI).
ETI is an accelerated and amplified PTI response, resulting in disease resistance and, usually, a hypersensitive cell death response (HR) at the infection site. At this stage pathogens can be grouped based on two different strategies: the first one changes the effector protein, while the second acquires additional effectors that suppress ETI. Subsequently, in phase five, plants respond with the generation of new R gene that recognize and bind the new developed effectors. The cycling between phases four and five is continuous and reflects the ongoing arms race between plants and their bioagressors (Walling, 2009).
Plant fitness can be greatly reduced if it spends energy to defend itself from injury. Most theoretical study such as those made Yamamura and Tsuji (1995) and by Poitrineau‘s workgroup (2004) have been focusing on the evolution of defence costs. Energetic costs can reflect in many aspects of plant life. First of all, resources invested in defences are unavailable for growth, development and reproduction; moreover, the reduced energy stocks could affect the defence itself, since the possibility of reduced attractiveness towards mycorrhizal fungi, pest predators as well as pollinators. Defence responses are expensive, so the commitment of defensive traits should decrease in the absence of enemies and should reach a very fast activation when necessary.

1.4 Plant responses against insects

Insects are a class of the animal kingdom with more than 750000 known species. They are divided into 30 orders split themselves into two main categories depending on wings presence. The insect body is encased in a hard capsule (tegument) which is a support for internal organs, it allows movement and ensures the control of evapotranspiration. Plants and insects coexist for millions of years and the majority of existing species feed on plants (Wu and Baldwin, 2010).
The insect body is divided into three parts: head, thorax and abdomen. On the head visual organs, sensory and the mouthparts are placed. Insect mouthparts may be divided into two main categories:

- Chewing or mandibulate
- Sucking or haustellate

The basic pre-oral structures of all insects have evolved from a generalized chewing apparatus, with the mandibles as the principals tearing and probing structures. Sucking mouthparts become from the chewing type by maxillae and mandibles elongation, and modified labium. Elongated chewing mandibles and jaws are merged to form a single thin and flexible tube, containing two channels: one with the function of taking nutritional liquids, the other causes the release of pre-digestive spittle. Thanks to this sucking apparatus, phloem feeders penetrate into the phloematic cells obtaining plant nutrients. Among this group of insects, aphids are able to damage tomato causing relevant losses in crop production. Aphids produce two types of spit: the first can create a gelatinous wall around the stylet isolating it from plant tissues

facilitating penetration; the second one is directly injected into the vascular tissue releasing lytic enzymes and digestive contents allowing nutrient digestion (Walling, 2008). This kind of feeding produces minimal mechanical damage than the one caused by chewing insects. Plants respond to these various damages in different ways and involve different and interconnected hormone-dependent defence pathways. Piercing-sucking insects are used to make multiple assay bites on plant leaf before choosing the sucking site. Entering their stylet between cells in order to establish a feeding site, they minimize injury damages trying to escape plant defence responses (Gatehouse, 2002). Studies carried out by DeVos and colleagues (2005) have shown that the answers to sucking insects in terms of genes and plant pathways are different from those activated by chewing insects (DeVos et al., 2005).

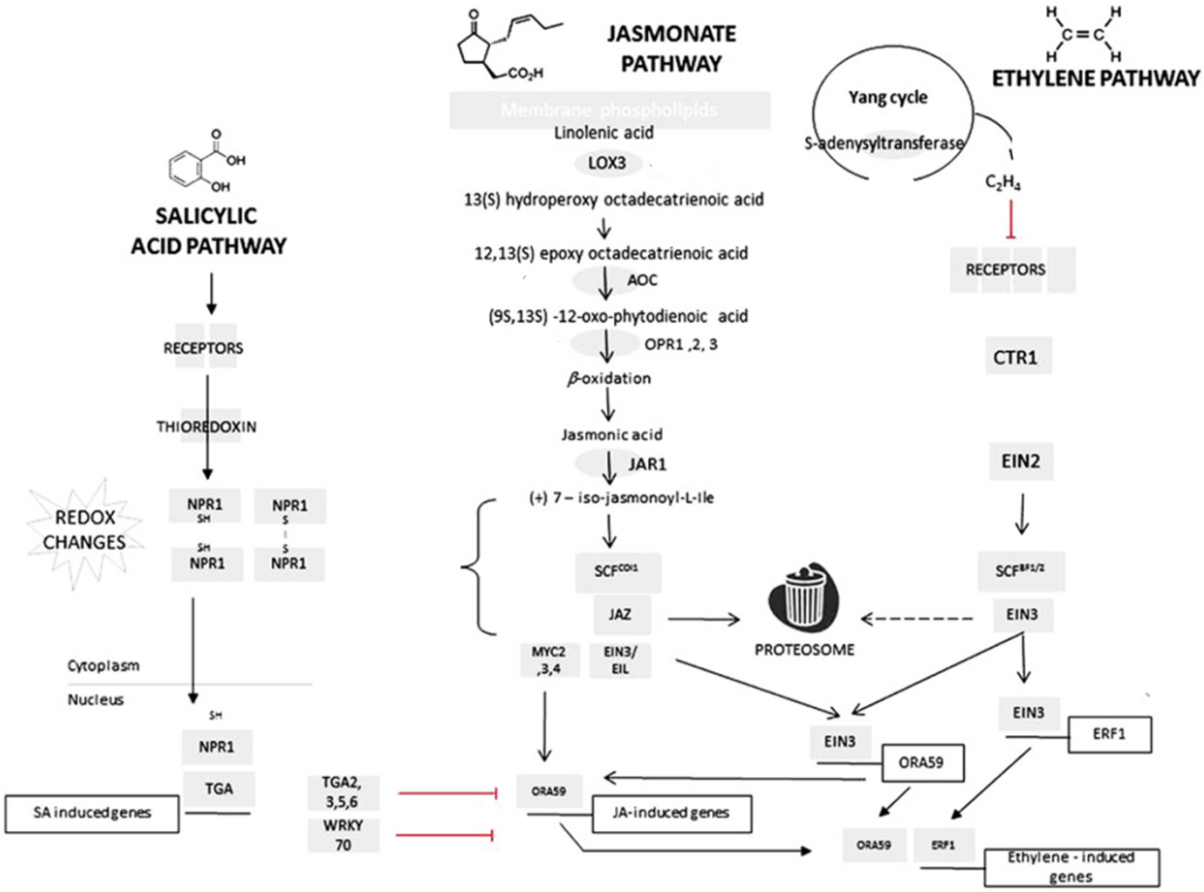


Figure 2: Plant herbivory-related pathways. Schematic versions of salicylic acid (SA), jasmonate (JA), and ethylene (ET) signaling cascade (Mur et al., 2013). Biosynthetic enzymes are represented as gray ovals and signaling components are gray rectangles. Abbreviations in the jasmonate biosynthetic pathway are as follows: LOX, lipoxygenase; AOC, allene oxide cyclase; OPR, oxo-phytodienoate reductase; for the ethylene biosynthetic pathway: ACS, 1-aminocyclopropane-1-carboxylic acid synthase; ACO, 1-aminocyclopropane-1-carboxylic acid oxidase. Genes and their regulatory promoters are represented as open boxes.

Plant responses against piercing-sucking insects, however, are very similar to those activated towards bacterial and fungal pathogens (Figure 2). Responses against this kind of insects range from extensive overlap with wounding to the promotion of SA-mediated responses (Kempema et al., 2007; Martinez de Ilarduya et al., 2003). In a time-course gene expression analysis after cabbage aphid infestation on *Arabidopsis* plants, Kusnierczyk and collaborators (2008) observed the regulation of genes

involved in ROS (Reactive Oxygen Species) production, SA- and JA-mediated pathways, senescence, cell wall organization and camalexin biosynthesis.
Phytophagous chewing activity produces cell-wall fragments and fatty acids, and causes the mixing of enzymes and substrates from different cellular compartments due to the cell disruption, which alerts the plant of a possible biotic attack. The fatty acid releasing from membranes induces JA pathway, known to be one of the most important plants defence line against herbivores (Figure 2). Its importance in resistance towards herbivores has been deeply studied using mutants impaired in JA synthesis or signalling (Bostock, 2005; Kessler and Baldwin, 2002; Sun et al., 2011).
Li and colleagues in 2004 showed that mutants impaired in Coronatine-Insensitive 1 (COI1) gene expression were weak in JA signalling processes resulting more susceptible to insect attack. COI1 encodes an F-box protein involved in the SCF-mediated protein degradation by the 26S proteasome and is required for most JA-mediated responses (Xie et al., 1998). Late products of octadecanoid pathway include antifeedant molecules such as proteinase inhibitors (PIs), peroxidises, polyphenol oxidase, leucine aminopeptidase and many other defence molecules which represents the real effectors of direct defences against herbivors.

1.5 Priming of defences

In vegetables, priming is a physiological process by which plants prepare to respond very quickly to future biotic or abiotic stresses (Frost et al., 2008). Ten years before, Katz introduced the concept of “primed state of the plant” as an augmented capacity to mobilize cellular defence responses (Katz et al. 1998). The “primed” state has been related by Conrath (2009) to an increased and more efficient activation of defence responses and an enhanced resistance to challenging stress.
The state of alert faced by plants can be induced by different signals that indicate the presence of the pathogen or parasite (Conrath et al., 2002), representing mechanism of induced resistance (IR) (Conrath, 2009). It has been recently observed that the activation of priming not only allows to trigger faster defences but also facilitates the processes of development of the plant (Conrath, 2011). The molecular mechanisms responsible for the pre-alerted state against herbivores are not completely understood but there are many studies with the aim to identify stimuli and beginning players of this mechanism. The wide variety of priming triggers (pathogens, pests, molecules of microbial origin, synthetic substances and abiotic stresses) suggests that the state of alert can be induced with multiple approaches (Pastor et al., 2014).
Molecular aspects of priming mechanism are related to the hypothesis that priming could be triggered by inactive cellular proteins that play an important role in cellular signal amplification. The subsequent exposition to biotic or abiotic stress factors could activate these dormant stored proteins forcing the activation and amplification of defence, immunity and stress tolerance (Figure 3). Signal amplification following MAMPs, DAMPs or HAMPs recognition involves MAP kinases 3 and 6 in *Arabidopsis* leaves after primary infection with the bacterial pathogen *Pseudomonas syringae pv. tomato (Pst)* (Beckers et al., 2009).
Another hypothesis on the molecular mechanism of priming proposed that chromatin modifications would prime defense genes for faster and stronger transcription (Bruce et al., 2007). These modifications could occur at defence genes loci for faster and more robust activation. During gene expression regulation, DNA and histones are subjected to covalent modifications such as methylation and acetylation. These chromatin modifications could slack the interaction of histones and DNA, thus

providing ‘open chromatin’ and/or docking sites available for transcription co-activators and chromatin remodelling factors. These processes could facilitate the recruitment of components of the general transcription machinery such as the RNA polymerase II complex and transcription factors, thus supporting transcription initiation and gene expression. Jaskiewicz and co-workers in 2011 demonstrated that the priming of *WRKY6* and *WRKY53* promoters required histones acetylation that facilitate their transcription upon future challenges. Hence, chromatin modification seems to provide a within-generation memory for priming in the systemic plant immune response (Conrath, 2015).

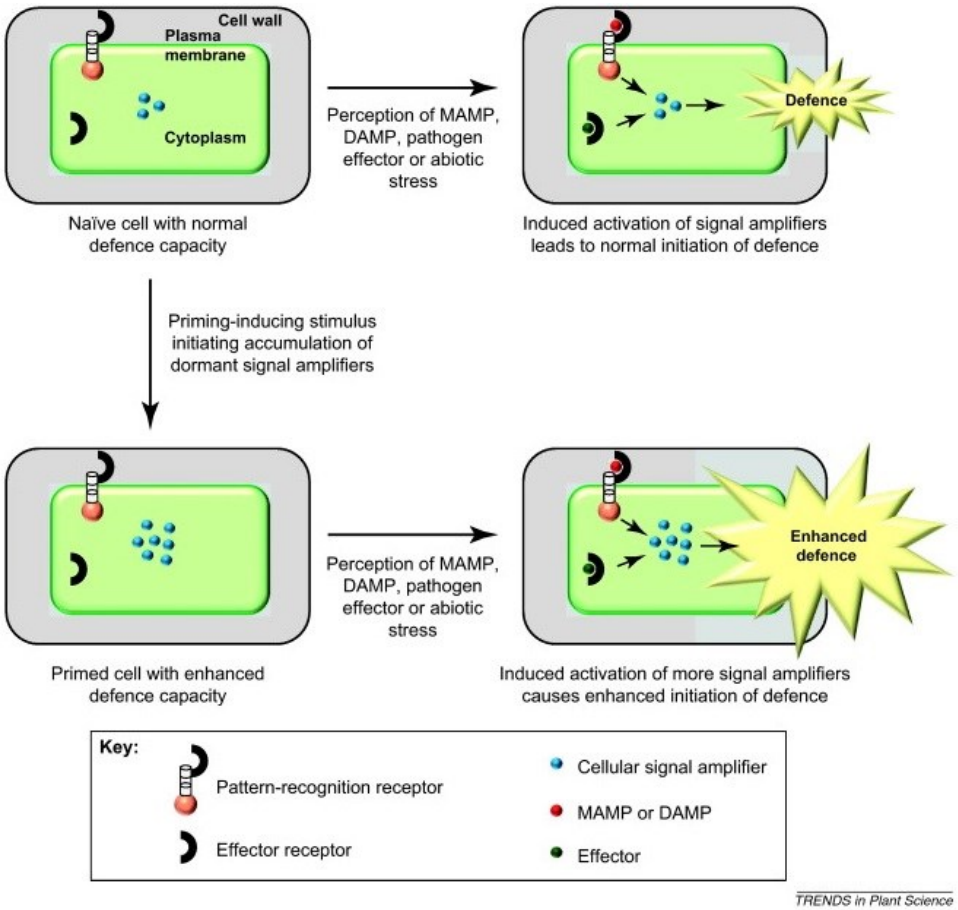


Figure 3: Accumulation of dormant cellular signal amplifiers as a probable mechanism for plant priming (Conrath, 2011).

Recent studies have shown the involvement of chemical signals associated with priming, including acetyl-salicylic acid (SA), SA analogs and JA (Thulke and Conrath, 1998). Novel signals identified in recent years include azelaic acid (AZA) and pipecolic acid (PA), considered indispensable for systemic priming and SAR.
AZA is a catabolite of free unsaturated fatty acids released upon localized bacterial infection (Jung et al., 2009) while pipecolic acid is a product by lysine degradation which is accumulated locally and systemically following the inoculation of *Arabidopsis* leaves with *Pseudomonas syringae* (Navarova et al., 2012). AZA is considered a mobile signal able to confer local and systemic resistance against bacterial agents. The upgraded tolerance mediated by AZA is due to higher accumulation of SA that could prime systemic defence upon bacteria rechallenge. Recent work suggested that the induction of priming and SAR by AZA requires glycerol 3-phosphate or a

glycerol 3-phosphate derivative (Yu et al., 2013). Navarová and colleagues (2012) observed that the degradation of lysine determined the production of pipecolic acid (PA), essential in priming of defense in Arabidopsis. They identified aminotransferase ALD1 crucial for PA accumulation, as the *ald1* mutant lacks PA synthesis and accumulation. This signal molecule was accumulated locally and systemically in *Arabidopsis* leaves following *P. syringae* inoculums. PA primed accumulating leaves formore robust biosynthesis of PA (but not SA), enhanced expression of the defense genes *ALD1*, *FMO1*, and *PR1*, and primed accumulation of the phytoalexin camalexin upon rechallenge (Navarová et al., 2012). Similar observations about pipecolic acid role in defence priming were reported by Vogel-Adghough and colleagues (2013) in tobacco.
In the last decade, VOCs have been discovered to play an important role in plant-to-plant airborne signalling: induced volatiles are known to mediate intra-plant and inter-plant communication and may warning an attack by herbivores. Kessler and collaborators (2006) studied VOCs function as airborne signals between neighbour plants. They studied the priming between damaged sagebrush and native tobacco, finding a higher mortality of *Manduca sexta* larvae on plants that have been previously exposed to clipped sagebrush. Exposure to VOCs from neighbouring attacked plants may allow the neighbours to be pre-alerted and to respond more rapidly if they are subsequently attacked. Interestingly, plants of different species are able to communicate via airborne signals (Figure 4), so priming signalling can overcome interspecies barriers (Kessler et al., 2006; Heil and Karban, 2009).

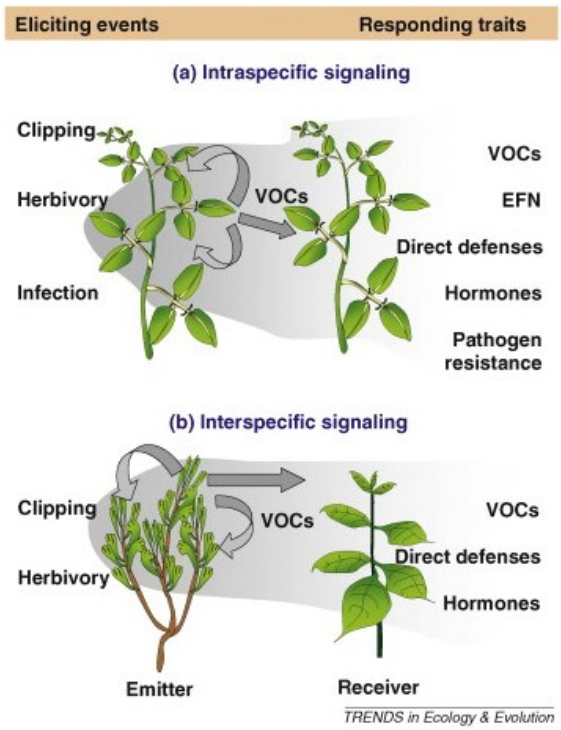


Figure 4: Physiological process of Priming and the important role of VOCs in plant-to-plant airborne signalling (Heil and Karban, 2009).

In response to wounding or herbivory, plants often change qualitatively and quantitatively volatile blend composition (Dicke and Loon, 2000; Mithöfer et al. 2005; Kost and Heil, 2006). In a pioneering study, Engelberth and his collaborators (2004) showed that maize seedlings previously exposed to certain volatiles from neighbouring plants and subsequently challenged by a combination of mechanical

damage and exposure to regurgitant of caterpillars of the beet armyworm (*Spodoptera exigua*), produced an higher sesquiterpenes and JA releases when compared to plants not exposed to the volatiles before.
In recent years, Ali and colleagues (2013) observed that corn plants exposed to a complex blend of herbivore induced plant volatiles (HIPVs) emitted by plants infested by the Northern armyworm led to DNA demethylation in the promoter of a trypsin inhibitor gene in the receiver plants. Upon Northern armyworm challenging, the transcription of the trypsin inhibitor gene was extraordinarily strong with the consequent long-lasting inhibition of worm larval development.
While VOCs of neighbouring plants damaged by herbivores may indicate a future risk, oviposition by herbivorous insects on the host plant is the most reliable predictor of future attacks. Deposition of insect eggs on plant hosts usually initiates a complex interaction that may lead to egg removal or killing, or to attraction of egg parasitoids (Conrath, 2015). Hilfiker and co-workers (2014) demonstrated that oviposition by the Large White butterfly, or treatment with its egg extracts, inhibits *P. syringae* multiplication in *Arabidopsis* by activating SAR response. In tomato, the application of *Helicoverpa zea* larval oral secretion primed JA accumulation and *PIN2* gene expression (Kim et al., 2012).
According to a recent study by Bandoly and colleagues (2015), insect oviposition often precedes an imminent attack, so plants can activate measures to increase their resistance against the developing larvae. In this study, *Nicotiana attenuata* plants have been exposed to oviposition of a generalist herbivore, *Spodoptera exigua* before a chewing assay. Treated plants showed less chewing damages compared to plants not treated by oviposition. So, it was inferred that the oviposition has increased plant responses to chewing damage.

1.6 Solanum lycopersicum defence: Systemin

Solanum lycopersicum belongs to *Solanaceae* and its origins are somewhat unclear, probably it comes from south-central America and arrived in the Mediterranean in 1500. This plant have annual fruits, medium size, usually creeping, which have rapidly developed, so it can grow in a couple of months, up to two meters long. The stems are thin, flexible, highly branched. Indeterminate tomatoes are characterized by their ability to grow continuously and produce fruit throughout the different seasons. Determined tomatoes are characterized by predetermined cycle. These tomatoes grow quickly reaching in few months the maximum height.
In the *Solanaceae*, a family of defense-related peptide hormones called systemins are involved in the activation of defense genes in response to wounding and herbivore attacks (Ryan and Pearce, 2003). Systemin (Sys) is a 18-amino-acid peptide hormone which is initially released at wound sites and it represents a primary wound signal in tomato (Figure 5). Sys is active at extraordinarily low levels (fmol/plant) and is thought to be released from a cytosolic precursor protein of 200 amino-acid called prosystemin (ProSys).
The tomato genome contains only one copy of the prosystemin gene; it is composed of 4176 bp and is structured into 11 exons, of which the last coding for systemin. The role of other exons has not yet been clarified but it was observed that they are organized in five repeated couples, assuming that the gene may have suffered several cycles of duplication and/or replication (McGurl and Ryan, 1992). Homologous sequences of this gene have been found in other species of the

Solanaceae family as potato and pepper, but not in tobacco, in which they were, instead, identified the functional homologues (Pearce et al., 2001). There were, in fact, identified three glycopeptides of 18 amino acids rich in hydroxyproline, called TobHypSys I, II and III, active in the induction of defence genes (Pearce et al., 2001). Even in tomato were identified three peptides rich in hydroxyproline which involved in the regulation of defence genes in a coordinated manner to sistemin, called HypSys I, II and III (Narvaez Vasquez et al., 2007), long respectively 20, 18 and 15 amino acids, derived from a precursor of 145 amino acids which includes a signal sequence and, as well as for peptides discovered in tobacco, are synthesized in the endoplasmic reticulum and the Golgi apparatus (Ryan and Pearce, 2003). Studies of over-expression and silencing of genes coding for these three peptides showed that they play a fundamental role in the regulation of defences induced by mechanical damage, indicating a concerted action with the systemin in the activation of defence mechanisms (Narvaez Vasquez et al., 2007).

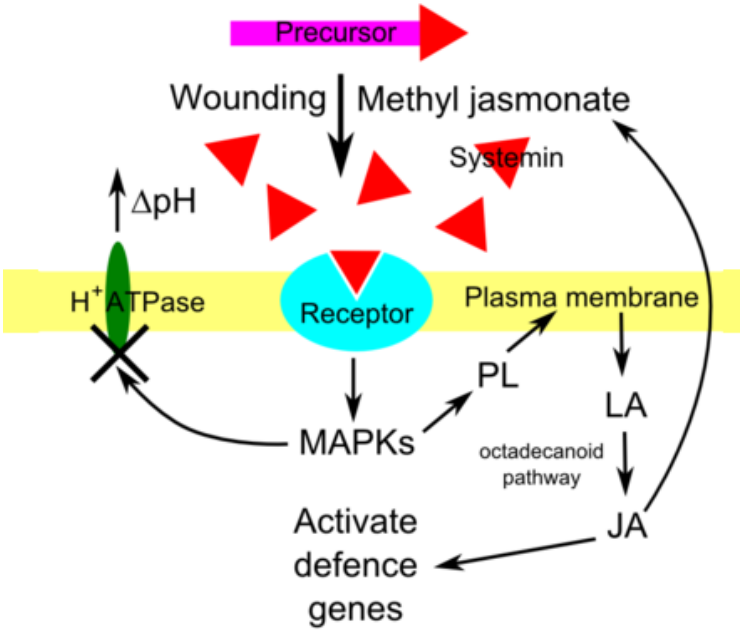


Figure 5: Systemin-mediated signal transduction pathway. MAPKs: Mitogen-activated protein kinases; PL: Phospholipase A; JA: Jasmonic acid; LA: Linolenic acid.

The activation of defense genes by systemin is mediated by the octadecanoid pathway, in which jasmonic acid (JA) and its derivatives are produced. Jasmonic acid is known to be involved as a signalling compound in multiple aspects of plant responses to their biotic and abiotic environment. After wounding or herbivory, systemin is released by ProSys through an unknown mechanism and it could bind a not yet identified receptor, probably located on cell-surface starting a complex intracellular signalling pathway that involves the activation of a mitogen-activated protein kinase (MAPK), the rapid alkalinization of the extracellular medium, the activation of a phospholipase A2, and the release of linolenic acid activating the above mentioned octadecanoid pathway. A previous study carried out in the host laboratory showed that the constitutive *ProSys* over-expression induces the modification of VOC blends making transgenic plants more attractive towards *Aphidius ervi,* an aphid parasitoid (Corrado et al., 2007). The same study showed

that *ProSys* over-expression was associated to the up-regulation of genes involved in the production of different VOCs such as members of the *LOX* family, *HPL* and *GCS*. Starting by these evidences, observing the impact of systemin-induced VOCs on neighbour plants and their effect on the activation of defence priming in tomato is a very interesting research field. As primed plants may exhibit a more efficient activation of defence responses (faster and/or stronger), systemin-mediated plant conditioning may represent a new tool for insect pest control.

1.7 Octadecanoid pathway

The complex cascade of reactions activated by the systemin or by wounding leads to the induction of the octadecanoid pathway in which jasmonic acid and its derivatives are produced (Schilmiller and Howe, 2005). Hydroperoxide lyase (HPL) starts a ramification in this pathway since the catalysis of linolenic and linoleic acids degradation in C_6 and C_{12} components. C_6 compounds are named “green leaf volatiles” (GLVs) and are parte of volatile bouquet released by plants.
Following various stimuli, such as elicitors coming from insects oral secretions or systemin or OGAs released by the damaged plant cell wall, hydraulic signals and membrane depolarization induce the activation of a signalling cascade headed by Phospholipase A2 (PLA2) activity. This enzyme releases linolenic acid from membranes which is converted by lipoxygenase (LOX) into 13-hydroperoxide. This compound can follow two pathways: hydrolysis by the enzyme hydroperoxidelyase (HPL) with the formation of GLVs or it can react with the enzyme allene oxide synthase (AOS) which converts the 13-hydroperoxide in an unstable epoxide then cycled by allene oxide cyclase (AOC) in the first cyclic compound, the fitodienoic 12-oxo-10,15 (Z) acid (OPDA), which results biologically active. After several reactions, including three steps of β-oxidation, the OPDA is transformed into jasmonic acid (Figure 6).
The abscisic acid (ABA) covers an important role in the activation of the early stages of this metabolic pathway, while auxins are negative regulators (Denancé et al., 2013). The salicylate can interact negatively with this pathway, inhibiting both the synthesis and action of jasmonic acid (Glazebrook, 2005). Ethylene is essential for JA-mediated wound-response gene expression (O’Donnell et al., 1996) but antagonizes JA induced nicotine production (Kahl et al., 2000).
In tomato, some of the genes encoding enzymes involved in the octadecanoid pathway have been isolated and cloned. For example, the gene encoding for lipoxygenase called as *TomLoxD* have been related to mechanical injury since its transcript is always detected in damaged leaves getting a strong increase in its expression following herbivory and treatment with systemin (Halitschke and Baldwin, 2003). The expression of the gene coding for allene oxide synthase, called *LeAOS,* increases in response to herbivores, locally and systemically (Howe et al., 2000). In tomato allene oxide cyclase (AOC) is encoded by a single gene and it is closely related to the activity of AOS; as for *AOS*, its expression increases in reply to mechanical injury, in proximal and distal tissues. Finally, the gene coding for the enzyme 12-ossofitodienoate reductase 3 (*OPR3*) in tomato presents three isoforms (Schaller and Stintzi, 2009). Among them, only one isoform, localized in the cytosol, shows activity in response to wounding, while the others remain at basal levels (Strassner et al., 2002). Stinzi and Schaller (2009) using mutant *opr3* demonstrated

that this enzyme cannot be replaced by other isoforms in its function, resulting highly specific (Stintzi and Schaller, 2009).

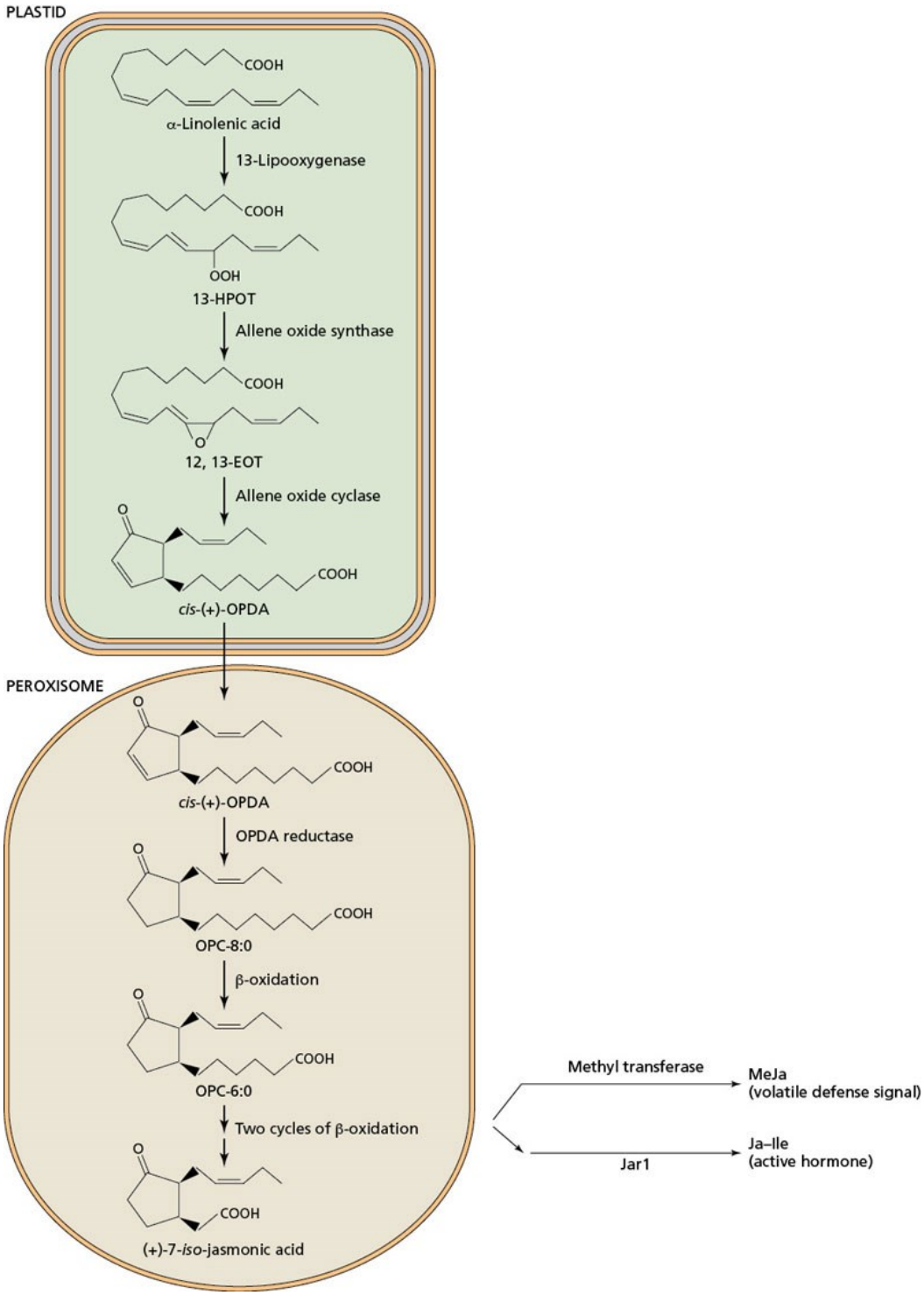


Figure 6: Representation of the octadecanoid pathway from α-linolenic acid (Acosta et al. 2009).

The octadecanoid pathway leads to the formation of several metabolites that can act directly and indirectly against a living organism. Examples of molecules induced by this pathway are polyphenol oxidase (PPO), lipoxygenase (LOXs), arginase, threonine deaminase (TD), leucine amino peptidase, phosphatases acid, a large number of protease inhibitors (PIs) classes, and several volatile compounds such as

(E) -β-farnesene, (E) -α-bergamotene, (E) -β-caryophyllene and other sesquiterpenes (Howe and Jander, 2008).

1.8 Research Objective

The effectiveness of systemin in promoting crop defences has been well documented over the past years. Transgenic plants, constitutively expressing *ProSys*, show a wide transcriptome reprogramming which reflects in enhanced defence responses which reduce herbivorous larvae growth and vitality and fungi damages (Coppola et al., 2014). In addition, these plants showed improved indirect defenses, producing a large amount of volatile compounds involved in the attraction of pests parasitoids (Corrado et al., 2007).
Here the contribution of Systemin in plant-to-plant communication finalized to the activation of defense priming in tomato plants is investigated.

2. MATERIALS AND METHODS

2.1 Plants Material

Seeds of *Solanum lycopersicum* cv. “Red Setter” were germinated in Petri dishes containing wet filter paper discs and placed in a growth chamber at 24±1 ℃ and 60% RH in darkness for 6 days.
Once the seeds were germinated, they were transferred to a polystyrene plateau containing barren substrate S-type (Floragard), in a growth chamber at 24±1 ℃ and 60% RH with a photoperiod of 16:8 light:dark, with brightness of 5000 lux. After a period of approximately 2 weeks, plants were transferred to pots of diameter of 9 cm containing sterile soil and grown for about 2 weeks with the same growing conditions.

2.2 Molecular characterization of transgenic plants

Genomic DNA was extracted from leaf cells following the Fulton protocol (Fulton et al., 1995): 2 leaf discs were collected and powdered using liquid nitrogen. “Microprep buffer” was prepared with 2.5 parts of DNA extraction buffer (0.35 M sorbitol, 0.1 M Tris-base, 5 mM EDTA, pH 7.5), 2.5 parts of lysis buffer (0.2 M Tris-HCl, 0.05 M EDTA, 2 M NaCl, 2% CTAB), 1 part of sarcosyl 5% (w/v) and 0.2 g of sodium bisulfite. 750 µl of Microprep buffer were added to samples, shaked and incubated at 65°C for 30-120 min. The tubes were filled with chloroform and mixed well by inversion. The tubes was centrifuged at 10000 rpm for 5 min and later the upper phase was removed and transfered to new Eppendorf tubes. 1 volume of cold isopropanol was added and tube content was inverted until the DNA precipitated. They were centrifuged at 13000 rpm for 5 min and the pellets were dried. Pellets were washed with ethanol 70%, centrifuged as above and allowed to dry well. The DNA was resuspended in 50 µl of sterile water and incubated at 65ºC for 10 min.
DNA was quantified by electrophoresis on agarose gel 0,8% (w/v) compared with known quantities of DNA of phage λ (Life Technologies), prepared as indicated in Table 1.

Table 1: Quantity ladder preparation: phage λ DNA.

Amount of DNA of phage λ	DNA λ (50 ng/µl)	DNA Loading buffer 10X	H_2O
50 ng	1 µl	2 µl	9µl
100ng	2µl	2µl	8µl
200ng	4µl	2µl	5µl

Samples were prepared with Loading Buffer (12:25% (w/v) bromo phenol blue, 0,25% (w/v) xylene cyanol, 00:30% (w/v) glycerol in water). A 80V potential difference was applied for 30 min. DNA bands were visualized using UV light (UV Gel Doc BIORAD) and samples concentration was estimated comparing their fluorescence with λ DNA bands. 150 ng of the extracted DNA were added to 10 µl GoTaq 5X Buffer (Promega), 0.4 µl of 25 mM dNTP, 2.5 µl of both 10 µM primers BBSBB FwRbcS Rv (Table 2) and 0.1 U GoTaq (Promega). The reaction mixture was brought to a final volume of 50 µl with distilled water and incubated in the Veriti Thermal Cycler (Applied Biosystems). An aliquot of 10 µl of the amplification products were prepared with 2 µl of 6X Loading Dye and were then loaded onto 1.2% (w/v)

agarose gel. The electrophoresis was performed by applying a potential difference of 5 V/cm for 45 minutes and the visualization of the bands was obtained as previously described. The size of the amplification products was determined by comparison with the molecular marker 1Kb Plus DNA Ladder (Life Technologies).

Table 2: List of primers and amplification conditions

Primer	Sequence (5'→3')	Tm[1]	Gene Name	Accession Number	LA(bp)	NR
EF Fw Rt	CTCCATTGGGTCGTTTTGCT	62	*EF1-α*	X53043	101	40
EF Rv Rt	GGTCACCTTGGCACCAGTTG	64				
BBSBB Fw	GGGAGGGTGCACTAGAAATA	58	*ProSys*	M84801.1	110[2]	40
BBSBB Rv	TTGCATTTTGGGAGGATCAC	58		M84800.1	717[3]	
BBSBB Fw	GGGAGGGTGCACTAGAAATA	60	*ProSys*	M21375	161	30
RbcS Rv	TTGTCGAAACCGATGATACG	62				
InhI Fw	GAAACTCTCATGGCACGAAAAG	64	*InhI*	K03290	114	40
InhI Rv	CACCAATAAGTTCTGGCCACAT	64				
nhII Fw	CCAAAAAGGCCAAATGCTTG	58	*InhII*	K03291	116	40
InhII Rv	TGTGCAACACGTGGTACATCC	64				
StbEF Fw	AAGCTGCTGAGATGAACAAG	58	*EF1-α*	X14449.1	687[2]	30
LeEF Rv	GTCAAACCAGTAGGGCCAAA	54		X53043.1	767[3]	
GCS Fw	TTGGTGAAGCCTTAACTCAGCC	66	*GCS*	AF035631	102	40
GCS Rv	GCAAATGGTGGTGTGCATCAT	62				
LoxA Fw	ATACACATGCTGTGATCGAGCC	66	*LoxA*	U09026	100	40
LoxA Rv	TGTGTCCCGGAAATGAGGAT	60				
LoxC Fw	TTGCCTATGGTGCTGAATGGA	62	*LoxC*	U37839	101	40
LoxC Rv	CAAGCCATGTGGTTCATTTGG	62				
LoxD Fw	TTCATGGCCGTGGTTGACA	58	*LoxD*	U37840	101	40
LoxD Rv	AACAATCTCTGCATCTCCGG	60				
MPK1 Fw	TTTTGATTGTCGGAATGCCG	58	*MPK1*	AJ535702	101	40
MPK1 Rv	CCTCCAGTACATTCTCCGAAC	64				

WRKY Fw	GAAAGACAGGCAGCCACTAGGA	68	*WRKY40*	AK326455	103	40
WRKY Rv	GCCCATCCCATTTTCACGT	58				
AOS Fw	GATCGGTTCGTCGGAGAAGAA	68	*AOS*	AF230371	101	40
AOS Rv	GCGCACTGTTTATTCCCCACT	66				

LA: length amplicon. NR: number of cycles. Tm: melting temperature [1] calculated on according to the rule of Wallace: 4ºC for G and C, 2 ° C for the A and T (Wallace et al., 1999); [2] Produced obtained by amplifying the transcribed mRNA; [3]Produced obtained by amplifying genomic DNA

2.3 Expression analysis of genes induced by biotic stimuli

2.3.1 *Spodoptera littoralis* chewing

The *S.littoralis* larvae were grown in a growth chamber at 25 ±1 °C, 70% of relative humidity (RH), with a photoperiod of 16:8 light:darkness hours. During their growth and development, larvae were fed with an artificial diet composed by 41.4 g/L corn germ, 59.2 g/L of yeast, 165 g/L of corn flour, 5.9 g/L of ascorbic acid, 1.8 g/L of methyl-4-hydroxybenzoate, 29.6 g/L of agar. Third and fourth instar larvae were let to feed on tomato plants for one hour and then were removed. Leaf samples were collected at different time starting from the moment in which the larvae were placed on the leaves. The samples were immediately frozen in liquid nitrogen and used for RNA extraction and gene expression analysis. Three biological replicates were analyzed for controls and treatments.

2.3.2 Tomato plants treatment with Systemin peptide

'Red Setter' plants have been treated with the Systemin peptide (Sys) synthesized at the Department of Chemistry of the University of Naples “Federico II” in professor Pedone workgroup. The peptide was dialysate in PBS 1X (137 mM NaCl, 2.7 mM KCl, 10 mM Na2HPO4, 2 mM KH2PO4; pH 7.4) and assayed in different concentrations (fM, nM, pM, uM) by applying 2µl in different points of fully expanded leaves. Leaf samples were collected after 6 and 24 hours from peptide foliar application and used for total RNA extraction. For each experiment three biological replicates were analyzed for controls and treated plants.

2.4 Exposure of plants to different sources

Solanum lycopersicum cultivar "Red Setter" were exposed to volatiles released by different plant sources. The experiment involves the analysis of three thesis summarized in Table 3.

Table 3: Thesis for the study of defense priming in tomato plants

Thesis	Source	Receiver
1	S1:RS chewed by *Spodoptera littoralis*	R1: “Red Setter”
2	S2: Transgenic plants constitutively expressing *ProSys*	R2: “Red Setter”
3	S3: RS treated with peptide Sys	R3: “Red Setter”
Control	S4: “Red Setter”	R4: “Red Setter”

RS: "Red Setter". Thesis 1: plants "Red Setter" R1 are exposed volatiles released by "Red Setter" plants chewed by *Spodoptera littoralis*; Thesis 2: R2 plants are exposed to volatiles released by transgenic plants over-expressing Prosystemin; Thesis 3: R3 plants are exposed to "Red Setter" plants treated with 100 pM Sys peptide.

Plants Sources have been used as a producers of volatile compounds. For the thesis N. 1, four weeks-old "Red Setter" plants were treated with four instar *Spodoptera littoralis* larvae. The treatment consisted in one hour of feeding on tomato plants, larvae removal and usage of this chewed plant as VOCs source. For the second thesis, transgenic tomato plants constitutively expressing *ProSys* cDNA (Coppola et al., 2014) were grown for four weeks in a controlled environment as described before (paragraph 2.1). VOCs emitted by 4 weeks-old transgenic plants were used to treat tomato receiver plants (R2). For the thesis N. 3, "Red Setter" plants were treated with systemin peptide and used as VOCs source to condition receiver plants R3 24 hours following peptide application. Sources and receiver plants were grown in separate chambers as previously described (par. 2.1).
Plants exposure to volatiles emitted from the three above mentioned types of sources was performed in a closed system constituted by air-thight boves in which receiver plants were exposed to the respective source in a 1:1 ratio (Figure 7). Each thesis has been developed in a separate box, each one arranged in a controlled environment in order to reproduce the optimal environmental conditions. The exposure occurred for a total of 48h. Leaf samples were collected from receiving and control plants and immediately frozen in liquid nitrogen at different time points: 3h, 6h, 9h, 24h and 48h.

Figure 7: Ari-thight boxes in which receiver plants were exposed to the respective sources.

2.5 RNA Isolation and Quantification

Total RNA was prepared from leaves by a phenol/chloroform extraction and a lithium chloride precipitation. In order to extract a high quality RNA, leaves were cut and immediately frozen in liquid nitrogen. 0.5 g of leaves were powdered in nitrogen liquid using mortars and pestles. 750 µL of RNA extraction buffer (100 mM Tris-HCl pH 8.5, 100 mM NaCl, 20 mM EDTA pH 8.0 and 1% SDS) and 750 µL phenol/chloroform 1:1 were added to leaf powder, immediately vortexed and centrifuged at 13000 rpm at 4°C for 5 min. Phenol/chloroform extraction was repeated two times on the aqueous phase and then a chloroform extraction was carried out in the same conditions. Nucleic acid precipitation was obtained by adding 750 µL of isopropanol, incubation in ice for 5 min and centrifugation at 13000 rpm at 4°C for 10 min. Supernatant was removed and the pellet was, firstly, dried and then suspended in 400 µL of DEPC-treated water (DEPC- Diethylpyrocarbonate; Sigma). RNA selective precipitation was obtained through the addition of 1 volume of 4M Lithium Chloride (Sigma Aldrich) and incubation on ice over-night. Samples were centrifuged at 13000 rpm at RT for 20 min, supernatant was discarded and pellet was suspended in 400 of DEPC-treated water. The addition of 0.1 volume of 3M Sodium Acetate pH 7.2 and 1 volume of 96% ethanol, the incubation at -80°C for 10 min and the centrifugation at 13000 rpm at 4°C for 10 min promote the precipitation of RNA. Pellets were finally suspended in 42 µL of DEPC-treated water. RNA samples were analyzed quantitatively and qualitatively by NanoDrop ND-1000 Spectrophotometer (NanoDrop Technologies). RNA concentration was calculated using he following formula (1):

[1] 1 OD260nm= 40 µg/mL

RNA integrity was checked by electrophoresis on a 1.2% agarose gel prepared with addition of Gel Red. 2 µg of each sample were prepared with 20 µL of 10 X RNA Loading Buffer (400 µL Formamide, 120 µL 37% formaldeyde, 5 µL loading buffer 10X) and treated at 65 °C for 5 min. After denaturation, samples were loaded on the gel and a 50V potential difference was applied for 20 min. DNA bands were visualized using UV light (UV Gel Doc BIORAD). Isolated RNA was treated with DNAse I to remove DNA contaminations. Two µg of RNA were added with 1X DNAse I Reaction Buffer (Life Technologies), 1 U DNAse I Amplification Grade (Life Technologies) and sterile water until a final volume of 10 µl. After the incubation at RT for 15 min, reaction was stopped by adding 1 µl of 25mM EDTA and heat treatment at 65°C for 10 min.

2.6 RNA retrotranscription

First strand-cDNA synthesis was performed using SuperScript II Reverse Transcriptase™ (Life Technologies) following this procedure: addition of 250 mM oligo dT primer, 0.5 mM dNTP mix and heating at 65°C for 5 min; quick chilling on ice and collection of tubes content by brief centrifugation; addition of 1X First Strand Buffer, 10 mM DTT, and incubation at 42°C for 2 min; after the addition of 200 U SuperScript II RT™ mix was still at 42°C for 60 min and reaction was finally stopped at 70°C for 15 min. The amplification of the cDNA region coding for EF-1α gene, a ubiquitously expressed gene (Shewmaker et al., 1990), was performed as control of cDNA synthesis and of DNA contamination presence since primers used for the PCR reaction, StEF Fw and LeEF Rv (Table 2), are localized in two contiguous exons

(Corrado et al., 2007). PCR products were visualized by electrophoresis: samples were loaded on a 0.8% (w/v) agarose gel prepared with the addition of GelRed in 1X TAE buffer (40 mM Tris-Acetate, 1mM EDTA) (Sambrook et al., 1989) and a 80V potential difference was applied for 30 min. DNA bands were visualized using UV light (UV Gel Doc BIORAD).

2.7 Real Time RT-PCR

Real Time RT-PCR was performed using Corbett Rotor Gene 6000 (Corbett Research). Reactions (total volume 10 µL) were prepared with 5 µL of the SYBR Green PCR Kit 2X (Qiagen), 0.3 µM of each primer, 1 µL of 1:20 diluition of first strand cDNA template. Amplifications were carried out using 2 technical and 3 biological replicates. The thermal cycling program started with a step of 10 min at 95°C, followed by 45 cycles of a 30 sec step at 95°C, 30 sec at Ta temperature (calculated as Ta= Tm-5, but often using a Ta gradient PCR), 15 sec at 72°C, followed by a dissociation kinetic analysis to assess the specificity of amplification reaction. Primers, designed with the aid of the Primer Express 2.0 software (Applied Biosystem, Foster City, CA) were chosen to amplify a fragment of approximately 100 bp. Relative quantification of gene expression was carried out using the $2^{-\Delta\Delta Ct}$ method (Livak and Schmittgen, 2001), where $\Delta Ct = Ct_{\text{target gene}} - Ct_{\text{reference gene}}$. The housekeeping gene *EF-1α* was used as an endogenous reference gene for the normalization of the expression levels of the target genes. The amplification of *EF-1α* interested the region delimited by EF Fw Rt and EF Rv Rt primers (Table 2). The statistical significance of the results was evaluated using the t-Student's test. Genes under investigation include: *ProSystemin (ProSys) (*acc. Num.M84801), *Germacrene C synthase (GCS)* (acc. Num. AF035631), *Tomato leaf wound-induced proteinase inhibitor I (TomInhI)* and *Tomato leaf wound-induced proteinase inhibitor II (TomInhII)* (acc. num. K03290 e K03291), *Lipoxygenase A (LoxA), Lipoxygenase C (LoxC)* and *Lipoxygenase D (LoxD)* (acc. Num. U09026, U37839 e U37840), *Mitogen-activated protein kinase 1 (MPK1)* (acc. Num. AJ535702), *WRKY40 (acc num* AK326455), *Allene oxide synthase (AOS)(acc num.* AF230371).

2.8 Bioassays

2.8.1 *Spodoptera littoralis* rate increase assay

S. littoralis larvae were grown in an environmental chamber at 25°C with RH 70% under 16:8 light/dark photoperiod on artificial diet composed by 41.4 g/L wheat germ, 59.2 g/L brewer's yeast, 165 g/L corn meal, 5.9 g/L ascorbic acid, 1.8 g/L methyl 4-hydroxybenzoate, 29.6 g/L agar. First instar larvae were transferred into plastic boxes containing vermiculite for pupae development. Leaf discs of Priming Conditions and control plants were daily supplied to experimental groups of 32 newly hatched larvae of *Spodoptera littoralis* and maintained at 28°C in plastic trays, containing a thin layer of a 2% agar solution, and closed with transparent plastic covers (CD International). Larvae were weighted everyday starting on day 3 from the beginning of the bioassay and mortality was daily checked during the whole larval feeding period. Statistical analyses were performed with the Graphpad Instat 3.0 software.

2.8.2 Analysis of attractiveness towards the parasitoid *Aphidius ervi*

The parasitoid *Aphiudius ervi* (Haliday) (Hymenoptera: Braconidae) was bred on its natural host *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae), maintained on beans plants (Vicia faba L. Angiospermae: Leguminosae, cv. Aquadulce) disposed in a jar. Aphids and parasitoids cultures were carried out separately in a growth chambers at 25 ± 1 ° C, 65 ± 5% relative humidity, with a photoperiod of 18 hours of light and 6 hours of darkness as previously described (Guerrieri et al., 2002).
Females used for the experiments were fed with a solution containing 50% honey and have been used between the first and the second day from their birth. All experiments were conducted between the third and the seventh hour from the start of light-phase.
Flight behavior of *A. ervi* towards tomato plants was analyzed using a single-choice wind tunnel bioassay. Parasitoid females were tested for each target by releasing them individually in the odour plume 35 cm downwind from the target. Parasitoids were observed for a maximum time of 10 min. Behavioral experiments were conducted on several days. In a wind tunnel bioassay, the receiver plants of each thesis were tested. The percentage of response (oriented flights, landings on the target) to each target was calculated. The number of parasitoids responding to each target in any experiment was compared by a G test for independence with William's correction (Rohlf and Sokal, 1995). This evaluation focused on the matters of direct flights oriented and landings of aphids on the plant receiving the three conditions. The resulting values of G were compared with the critical values of x2 (Rohlf and Sokal, 1995).

2.9 Qualitative and quantitative evaluation of volatile blend modifications using GC-MS

VOCs from receiver and source plants were collected by an air-tight entrainment system immediately after the wind-tunnel bioassay. Single plants were placed into bell jars sealed with Parafilm and connected to a circulation pump whose flow was adjusted at 200 ml/min. Before reentering the pump, the air passed through an adsorbent trap made of Tenax (Cat. no. 226-336, SKC, Eighty Four, PA, USA) connected to the system by a Teflon-capped glass plug. In order to reduce any stress to the plant in the system, each collection lasted 3 hr. Air entrainment volatiles were separated by an integrated system including thermal desorber (Tekmar TD-800), gas chromatograph and mass spectrometer.
For each thesis were collected volatiles emitted from source and receiver plants. Gas chromatography–Mass spectrometry (GC-MS) is a method that combines the features of gas-liquid chromatography and mass spectrometry to identify and quantify different substances within a test sample.

2.10 RNA-Sequencing and Data Analysis

Total RNA was extracted as previously described (Paragraph 2.5) from 3 receiver plants exposed to volatiles emitted by an equal number of source plants referring to thesis N. 3 and N. 4 for control plants (Paragraph 2.4). RNA samples were analyzed quantitatively and qualitatively by Bioanalyzer (Agilent Technologies). RNA was converted to cDNA and sequenced on Illumina HiSeq1500 platform (external

service). A paired ends sequencing, 2 x 30 M of reads, was chosen. The process generates millions of short reads sequenced from both ends of each cDNA fragment (paired-end sequencing). The raw data for each sample consist of a long list of short sequences with associated quality scores (*fastq* format). All the steps following described have been performed for each biological replicates analyzed per sample. Quality evaluation was carried out through the FastQC software.
Adapters were removed using Trimmomatic software eith the subsequent mapping on the tomato reference genome, available since 2012 on Solgenomics platform (http://solgenomics.net/organism/Solanum_lycopersicum/genome). It is composed by 12 nuclear for a total of 950 Mbp with 34727 genes; among them the 56.6% is annotated with GO terms (19662). Mapping was performed using STAR software which allows multiple mapping of reads in very short time. Samstat software was used for another quality control before counting mapped reads using Counts tool. Following the raw data mining, differentially expressed genes among test and control were called using the intersection of results obtained by two statistical methods: EdgeR and NoiSeq. The fist one implements the Negative Binomial model for the analysis and quantification of the differential expression on "digital" data gene expression (digital gene expression or DGE) (Robinson et al., 2010). HTS filter was used to reduce the percentage of too variable or weakly expressed genes. The General Linear Model (GLM), which uses as a linear regression, was used to assess data statistical significance.
In parallel, the NOISEQ package which provides a correction algorithm for replicas variability, allowed to identify differentially expressed genes. The basic idea underlying NOISeq is that a given feature may be considered differentially expressed if their change in expression between two experimental conditions is greater (or has a higher probability of being greater) than the change observed among replicates within the same condition (Tarazona et al., 2013).

2.10.1 Gene Ontology and enrichment analysis (GOEA)

Functional annotation of differentially expressed genes (DEGs) was performed using two softwares: AgriGO and Blast2GO. The former is a tool for the association of ontology terms to genes, with special attention to agriculture-related species. The latter assigns GO terms to genes under analysis based on sequence similarity.
Fasta format sequences were downloaded from NCBI, the Tomato Gene Index (DFCI) and Plant Transcript Assemblies Database (TIGR). Annotation started with a blastx alignment followed by mapping and annotation steps. The analysis was enriched by the loading of Kegg pathways. Over-represented functional categories were identified through the Enrichment Analysis. Data statistical significance was calculated by Hipergeometric test which returns the P-value for each Gene Ontology category. The output is a table of functional classes associated with differentially expressed genes in order of FDR and the value of the enrichment score.

3. RESULTS

The first part of the research activity was oriented to the establishment of the optimization of the experimental conditions, assuming that VOCs perception by receiver plants would originate a modification in the level of transcripts of defense related genes (Arimura et al., 2000; Farag et al., 2005). It was initially evaluated the effect of VOCs on receiver plants in an environmental chamber. Under this experimental condition no modification in defense related genes expression was observed possibly due to the chamber aeration with consequent signal dilution. Although common tomato 'sentinel and soldiers' defense genes were analyzed (see par. 3.3), the increase of other transcripts or the production of defense related metabolites, cannot be ruled out. It was preferred to set up a different experimental condition for plant exposures. For this purpose, closed boxes were prepared. The boxes were covered by an inert material of a sufficient capacity to accommodate from 5 to 6 four weeks-old plants. Different exposure times were tested. The response of receiver plants to source exposures was characterized at molecular and biological levels. Molecular analysis focused on the variations of defense gene expression induced by VOCs perception in the receiver plants, while biological aspects dealt with the evaluation of the induced direct and indirect defenses in receiver plants. Three kinds of volatile sources were used: 1) Tomato plants following *Spodoptera littoralis* larvae chewing; 2) Transgenic tomato plants over-expressing Prosystemin cDNA; 3) Tomato plants following Systemin peptide foliar applications.
The first source was represented by plants chewed by *S. littoralis* larvae for 1 hour before exposure. In all cases, both groups of plants were grown separately in two different green houses set up in order to produce identical environmental conditions. For the experiment, treated tomato plants were combined with receiver plants (1/1 ratio) in the closed boxes. No contact between the two set of plants was allowed (Figure 8). Controls were represented by untreated plants exposed to other untreated plants in closed boxes.

Figure 8: Experimental conditions, receiver plants exposed to source plants in a closed box.

3.1 PCR screening of transgenic plants

Transgenic plants over expressing the Systemin precursor were already available (Coppola et al., 2014). Transgene presence of *ProSys* gene was verified in T1 plants by a PCR amplifying the gene sequence including the last exon and a portion of rbcS terminator using the primer pair BBSBB as forward sequence and rbcS as reverse sequence (Table 2). Genomic DNA was extracted from leaves and quantified by comparison with known amounts of DNA of phage λ (Life Technologies) through electrophoresis on agarose gel 0.8% (w/v). Figure 9 shows an example of genomic DNA quantification.

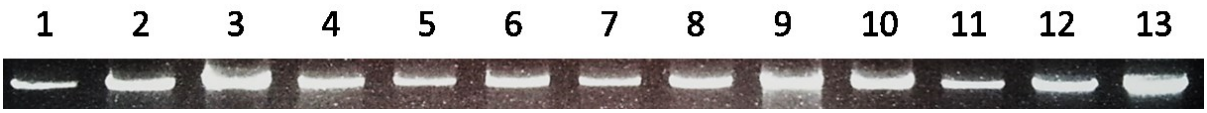


Figure 9: Electrophoresis of genomic DNA extracted. Lane 1-10: genomic DNA extracted from some samples RSYS (indicated in the figure). Lane 11-13: DNA of phage λ, respectively 50 ng, 100 ng and 200 ng (Promega).

The isolated genomic DNA was used as template for a PCR screening: the expected amplicon size (161 bps) was obtained. Figure 10 shows an example of the PCR screening of DNA extracted from transgenic plants and untransformed controls. PCR positive plants were selected to be used as sources for the thesis n. 2 (Table 3).

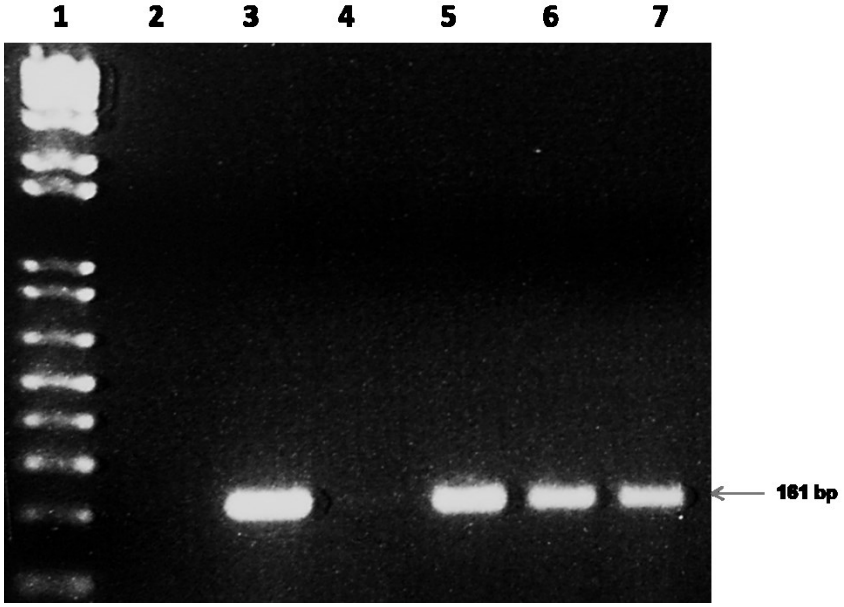


Figure 10: Electrophoresis of PCR products on agarose gel at 2% (w/v). Lane 1: Marker 1Kb Plus; 2: No template control; 2: control "Red Setter"; lane 3-7: different transgenic plants

3.2 Expression analysis of defense genes in sources plants

Prosystemin overexpressing tomato plants were previously characterized (Coppola et al., 2014). This study showed that transgenic plants constitutively activated defense responses. In addition, it was also demonstrated that the overexpression of the *Prosys* gene modify the blend of VOCs produced by transgenics in respect to control (Corrado et al., 2007). Therefore, these transgenic plants (RSYS) were used as source plants.

3.2.1 RNA and cDNA quality

Table 4 shows absorbance values relative to RNA quantification of a small group of samples. All samples contained reduced concentrations of proteins and contaminants such as phenols, carbohydrates and aromatic compounds. As shown by ratios A260/A280 and A260/A230 there are very close to 2. A value attributed to pure RNA.

Table 4: Concentrations and absorbance values of some RNA samples

Sample	Concentration [ng/µl]	A_{260}/A_{280}	A_{260}/A_{230}
RS/control	1003,76	2,22	2,20
Source S2	975,32	2,22	2,21
Source S3	1185	2,21	2,20
Receiver R1	800,05	2,24	2,21
Receiver R2	1158,01	2,22	2,20
Receiver R3	777,23	2,23	2,21

The electrophoresis on 1.2% (w/v) agarose gel was performed to assess the integrity of the extracted RNA (Figure 11).

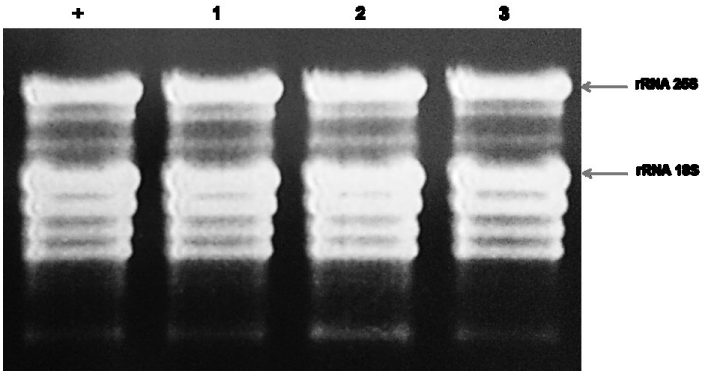


Figure 11: Agarose gel electrophoresis on 1.2% (w/v) of 5 µg of some RNA samples prepared from leaves of receiver plants.

RNA integrity was evaluated by the presence of clearly defined bands, and a good quality is ensured when the first band from the top to down (ribosomal RNA 25S) and third band (18S ribosomal RNA) exhibit fluorescence respectively twice than the other. Isolated RNA was used for the first-strand cDNA synthesis. To this purpose, a DNAse treatment was carried out to remove genomic DNA contaminations. The produced cDNA was analyzed by PCR using the primers StbEfFw and LeEfRv that are located between two consecutive exons of the gene *EF1-α*, constitutively expressed in all tomato plant tissues (Pokalsky et al., 1989). These primers allow not only to verify the quality of the synthesized cDNA, but also to further verify the absence of contaminant genomic DNA. In fact, the selected primers anneal on two contiguous exons, therefore producing different amplicon size depending on the kind of template: 765bp from genomic DNA template, 687bp from cDNA template. PCR products were separated on 1.5% agarose gel shown in Figure 12.

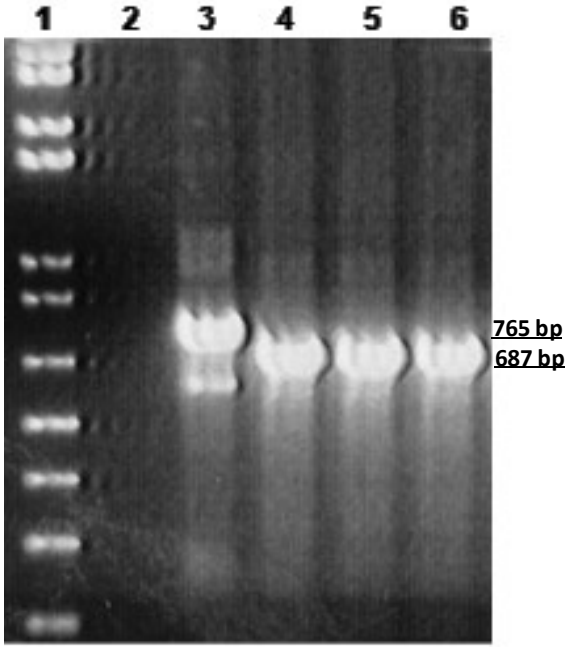


Figure 12: Electrophoresis on agarose gel 1.5% (w/v) of *EF-1α* gene amplification products obtained from some cDNA preparations. 1: marker. 2: No template Control; 3: amplicon of genomic DNA; lane 4-6: amplicons of cDNA samples.

The figure 12 shows that the prepared cDNA was of good quality and that no genomic DNA contaminated the RNA preparation. CDNAs were analyzed by Real-Time RT-PCR to monitor the expression levels of defense related genes selected according to their known involvement in plant defense responses. The relative quantification of gene expression was performed using as calibrator the cDNA prepared from 'Red Setter' control plants exposed to volatiles emitted by 'Red Setter' untreated plants (Thesis N. 4). The fluorescence data were standardized with those obtained by the amplification of the endogenous reference gene *EF1-α.* Relative quantities of transcripts were calculated using the method of $2^{-\Delta\Delta Ct}$ (Livak and Schmittgen, 2001) that issues the RQ index (Relative Quantification).

3.2.2 Genes induced by leaves chewing from *Spodoptera littoralis*

In order to verify the expression of defense genes associated to insect pest's damage, a time-course expression analysis was carried out following *S. littoralis* larvae chewing on 'Red Setter' plants. One single larva was placed on each plant, and allowed to feed for one hour carefully observing that the chewing was confined to a leaf and that the damage, between the biological replicates, was uniform (Figure 13).

Figure 13: Larval chewing on tomato leaf. The wounding damage was confined to a leaf and uniform between the biological replicates

Chewed and distal leaves were then harvested at different time points for gene expression analyses. The genes analyzed were early and late genes of the jasmonic acid pathway, associated with the responses induced by chewing insects (Ryan 2000; Gatehouse 2002; Corrado et al., 2007). Larvae chewing induced the expression of all the selected genes (Figure 14). The transcripts of the early genes *ProSys, LoxC* and *AOS,* as expected*,* increased rapidly and continuously only in the damaged leaves (Figure 14 a, b and c), while the transcript of the late gene *InhI,* increased both in the damaged and the distal leaves as shown in figure 14 d*.* Moreover, *InhI* transcript reaches its maximum expression level after 24 hr. This is explained considering that protease inhibitors provide a formidable barrier to protein digestion. Systemin signal transduction pathway appears to be a tomato plant strategy to amplifiy plant ability to mount an effective defense response against the attacking predators.

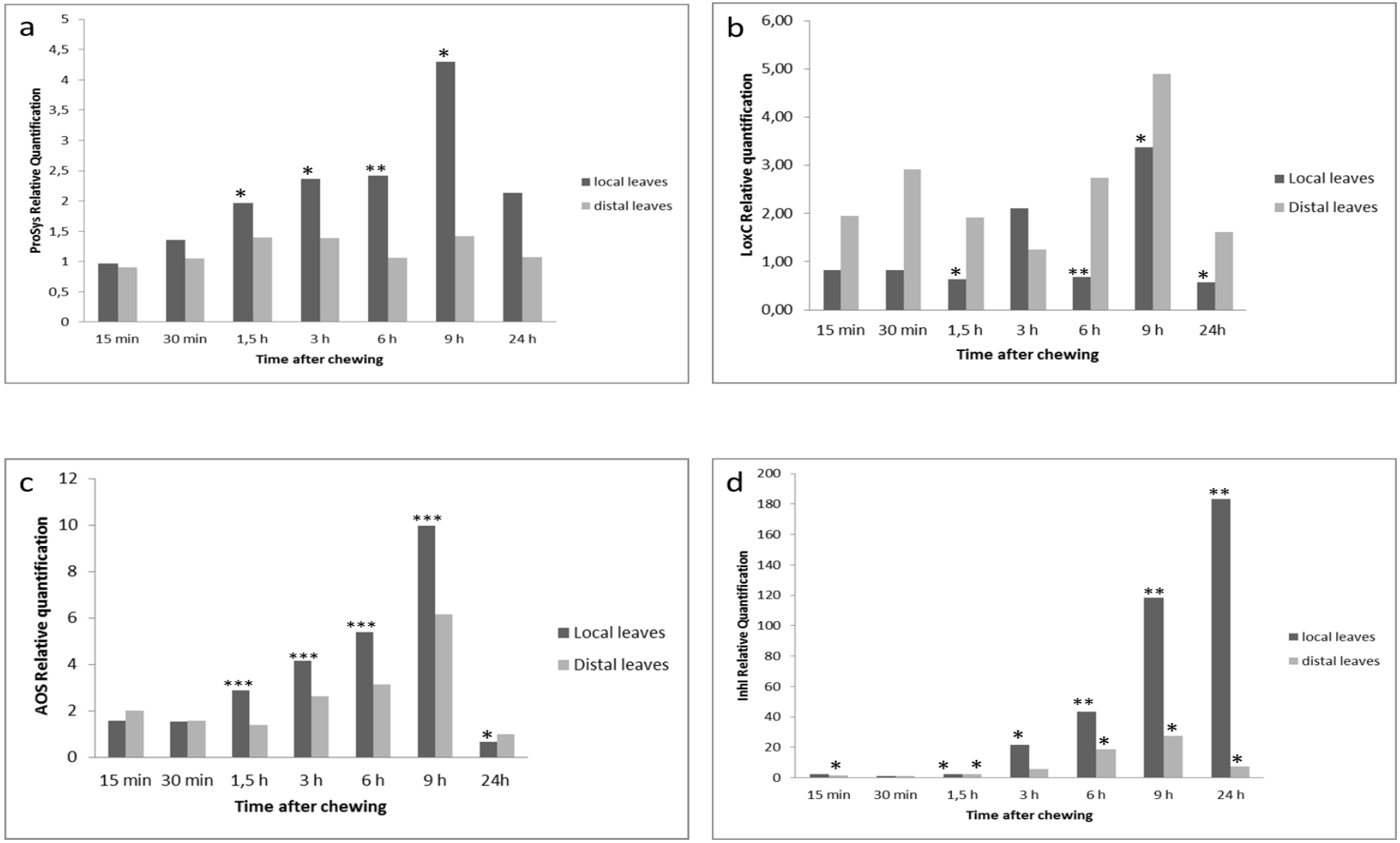


Figure 14: Relative gene quantifications of defense-related genes induced by *S. littoralis* chewing on local (dark gray) and distal (light gray) leaves of 'Red Setter' plants, in a time-course experiment. Asterisks indicate statistical significance verified with the Student's t-test (* P <0.05, **p<0.01; ***p<0.001).

3.2.3 Genes induced by foliar applications of Systemin peptide

The ability of the peptide to modulate gene expression, following applications of different peptide concentrations on intact leaves, was monitored analyzing the increase of defense related gene transcripts in treated leaves. Following the application of peptide in multiple spots, treated leaves were collected after 6h and 24 hours from the treatments to quantify *ProSys* and *InhI* gene transcripts.

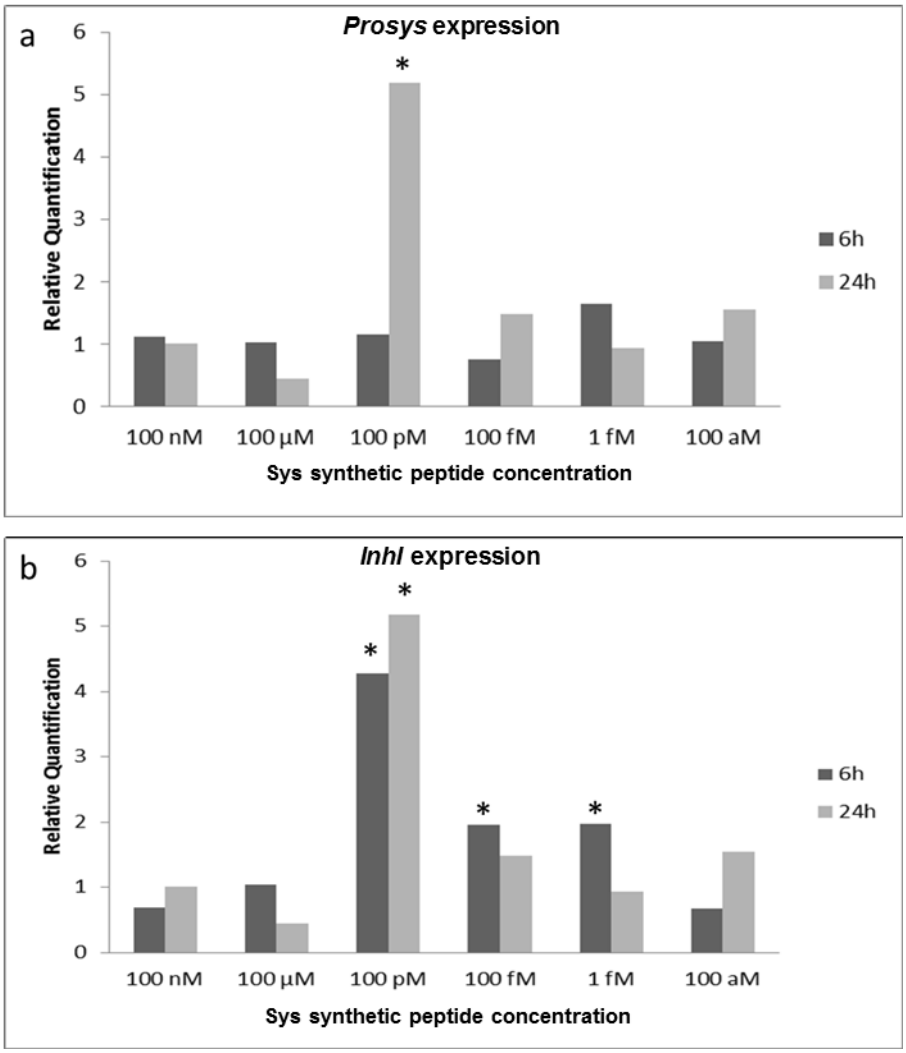


Figure 15: Relative quantification of *ProSys* (a) and *InhI* (b) genes induced by treatments with different concentrations of Systemin synthetic peptide. Quantities (RQ) are shown relative to the calibrator genotype 'Red Setter'. Asterisks indicate statistical significance, Student's t-test (* $p < 0.05$).

The time-course analysis of the *ProSys* gene transcript increase showed a strong induction at 24h from the treatment with 100 pM synthetic peptide concentration, while no effect was registered for any other concentration (Figure 15a). The expression of the *InhI* gene, conversely, was induced also by fM concentrations (Figure 15b). In addition *InhI* transcripts significantly increased after 6 and 24 hours from peptide application (Figure 15b) similarly to what observed after *S. littoralis* leaf chewing (Figure 14 d). The activation of *ProSys* and *InhI* genes under the described experimental conditions suggest that the peptide is internalized in the absence of damage or injury, or in some way it is perceived by leaf cells, according to a

mechanism not yet known, leading to the activation of defense genes. This is novel and important observation that supports the possible use of the peptide in IPM strategies.

3.3 Expression analysis of defense related genes in receiver plants

In order to verify the effect of source exposures on defense gene expression in the receiver plants, transcript increases of selected defense related genes were analysed by qReal Time RT-PCR. For this purpose, total RNA was isolated from fully expanded leaves of receiver plants and quantified by Nanodrop. The following table summarizes the priming theses used for the experiments:

Source	Receiver
S1: 'Red Setter' plants chewed by *Spodoptera littoralis*	R1: “Red Setter”
S2: RSYS plants	R2: “Red Setter”
S3: 'Red Setter' plants treated with Sys peptide	R3: “Red Setter”
S4: “Red Setter”	R4: “Red Setter”

The gene expression analysis was addressed to the study of molecular effect of airborne signals on plants to plants communication. Impact of systemin-induced VOCs blends on receiver plants was evaluated through a time-course expression analysis of a set of defense genes either involved in JA biosynthesis or activated by JA signalling pathway.
As previously mentioned, the exposure of receiver plants took place in a closed system for 48 hours and leaf samples were collected at different time points, 3, 6, 9, 24 and 48 h, for gene expression analyses. Early and late defense related genes involved in both direct and indirect defense mechanisms were selected for expression analyses: *GCS, InhI* and *InhII, LoxA*, *LoxC* and *LoxD, MPK1* and *WRKY40. GCS* is involved in the synthesis of terpenoids, the most abundant volatile compounds in plant that play an important role in the attraction of herbivorous insects parasitoids and predators therefore, promoting indirect defenses (Colby et al., 1998; Falara et al., 2011). *InhI* and *InhII* encode Protease Inhibitors, small proteins that inhibit the activity of digestive enzymes in the gut of the herbivore, therefore reducing insect growth and vitality (McGurl et al., 1994). *Lox* genes encode enzymes that play an important role in plant responses to herbivore damages. The most important features of LOX action are the metabolic end-products, being known as oxylipins. Such products have specific roles in signalling and plant defense response (Porta and Rocha-Sosa, 2002). Multiple isoforms of LOX have been detected in a wide range of plants (Feussner and Wasternack, 2002). In tomato, at least five *Lox* genes were isolated (Zhang et al., 2006). *LoxA* and *LoxC* expression is essential for the synthesis of specific VOCs (Shen et al., 2014). *LoxC* shows constitutive expression in the leaf. However, it appears to be involved in the leaf damage response because its transcript increased with mechanical damage (Halitschke and Baldwin, 2003). *LoxD* is rapidly induced by wounding therefore beeing strictly related to defense response (Hu et al. 2013). Moreover, *LoxC* and *LoxD* are targeted to chloroplasts the proposed major site for fatty acid hydroperoxide metabolism. *MPK1*, codes for a

kinase, that is a member of a wide family of early enzymes involved in signal transduction. It is generally accepted that systemin interacts with a receptor, not yet identified, starting a complex defense cascade that involve MAPKinases (Walling, 2009). *WRKY* genes belong to a superfamily including around a hundred of members encoding transcription factors (TF). Members of the family contain at least one conserved DNA-binding region, designated the WRKY domain, that include the highly conserved WRKYGQK peptide sequence. WRKY TF act in a complex defense response network as both positive and negative regulators (Eulgem and Somssich, 2007). A recent study has shown that some *WRKY* genes, in *Arabidopsis*, are involved in chromatin modifications that help the activation of the transcription of stress related genes (Jaskiewicz et al., 2011). Specifically, *WRKY40* functions as a positive regulator of resistance toward the necrotrophic fungi in *Arabidopsis* (Karim et al., 2015).

3.3.1 Expression profiles induced by *Spodoptera littoralis* chewed plants

One of the conditions in which the phenomenon of defense priming has been studied is the induction of direct and indirect defenses in plants exposed to volatiles emitted by injured plants (Holopainen and Blanke, 2012; Paré and Tumlinson, 1999; Song et al., 2013). It is well known that plants infested by herbivorous insects modify the VOC composition that activate between- and within-plant signaling cues inducing or priming defense responses in neighboring intact plants or intact parts on the infested plant. Therefore plants infested by *S. littoralis* were used as internal control of the experimental design.
Expression profiles of defense related genes in R1 plants are shown in Figure 16. Gene expression is modulated during the whole exposure time interval of 48 hours.

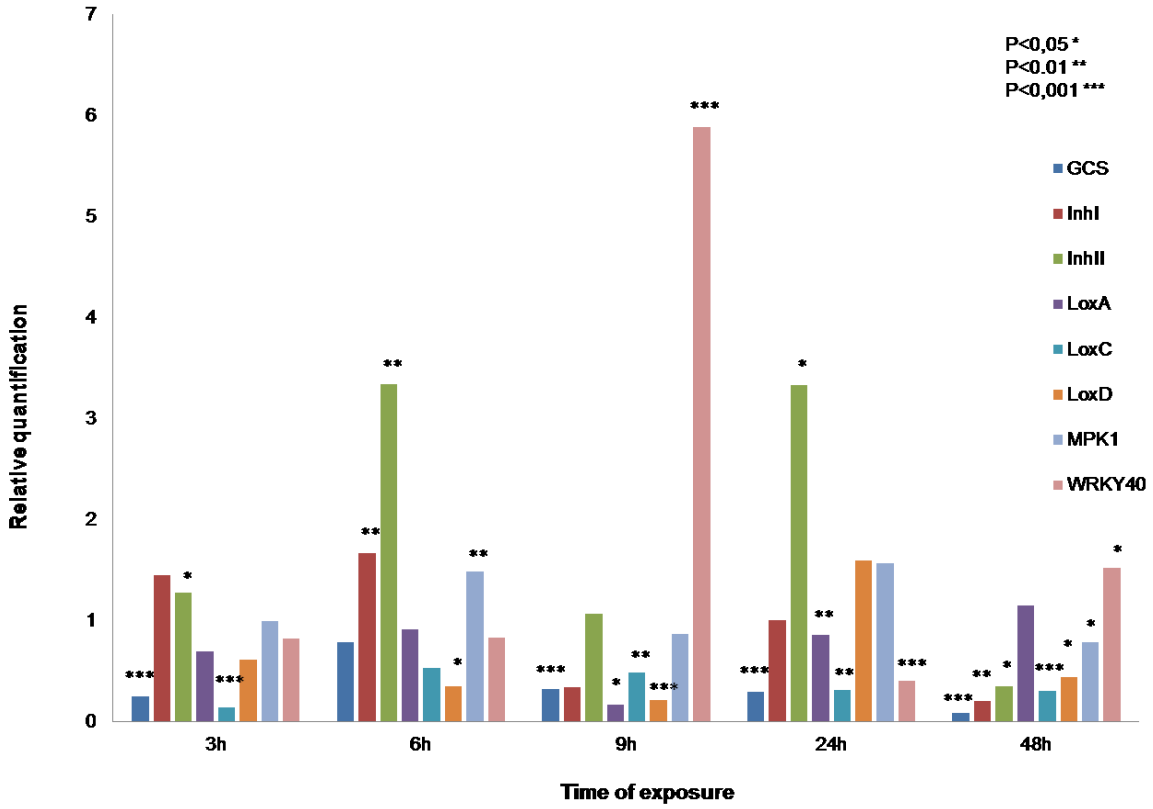


Figure 16: Relative Quantification of the genes expressed in the recipient plants exposed to plant chewed by *S. littoralis* evaluated at different time points. Asterisks indicate statistical significance, Student's t-test (* p <0.05; ** p <0.01; *** p <0.001).

The more relevant influenced transcripts encode for Inh I, Inh II and WRKY40, known for their involvement in responses to different stressors (Walling, 2009; Dicke and Baldwin, 2010). *InhII* over-expression occurred in several experimental time points (Figure 16). Together with *InhI* they are both significantly induced at 6 hours post exposure, indicating the activation in R1 plants of direct defense mechanisms. A consistent over-expression of *WRKY40* was observed after 9 hrs from exposure. This data suggest that in tomato WRKY40 TF is involved in the activation of direct defenses. These results confirmed that, in the designed experimental conditions, S1 plants modulate the R1 expression of some defense related genes.

3.3.2 Expression profiles induced by transgenic plants over-expressing the *ProSys* gene

It was previously observed that tomato plants overexpressing *ProSys*, RSYS plants, undergo a deep transcriptome reprogramming that constitutively activate a constant 'defense status' (Coppola et al., 2014). In addition, in was previously demostrated that VOC composition of RSYS plants are also deeply modified (Corrado et al., 2007). These results prompted to investigate if RSYS plants are able to prime defense responses in neighbouring plants.

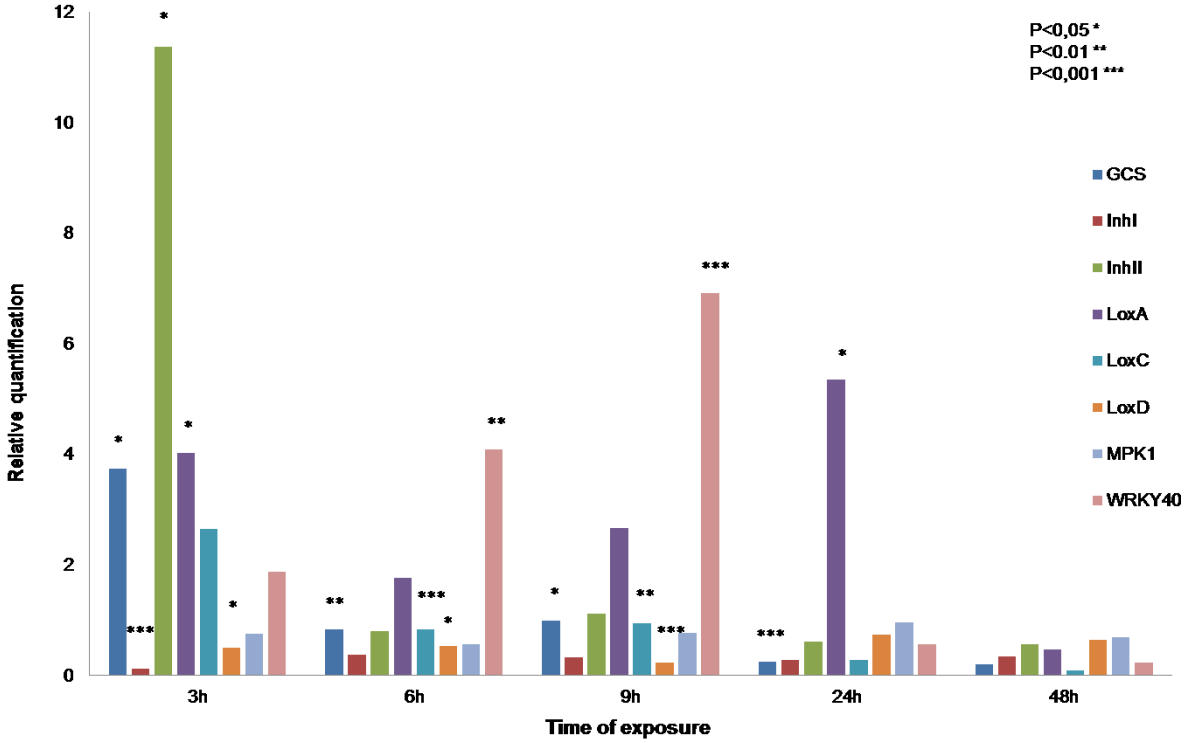


Figure 17: Relative Quantification of genes expressed in R2 receiver plants exposed to RSYS plants (S2) overexpressing evaluated at different time points. Asterisks indicate data statistical significance, Student's t-test (*p <0.05; **p <0.01; ***p <0.001).

The time-course expression analysis of the selected genes is shown in Figure 17. R2 plants showed a quicker and more intense defense response in comparison with that observed in R1 plants. Both genes involved in direct and indirect defense mechanisms are induced. Interestingly, *WRKY40* expression reaches its peak after 9 hours of exposure, similarly to what observed in R1 plants (Figure 16). These data demonstrate that constitutive expression of *ProSys* is able to prime defense responses in neighboring plants even in a more efficient way than plants chewed by insect larvae. This observation, however, can be due to the selected time of chewing. A longer feeding time of larvae might lead to a different result.

3.3.3 Expression profiles induced by plants treated with Systemin

In order to assess if systemin peptide foliar applications could influence the expression of defense genes in neighbour plants, the same time-course expression

analysis was carried out on receiver plants R3. The obtained results are shown in Figure 18.

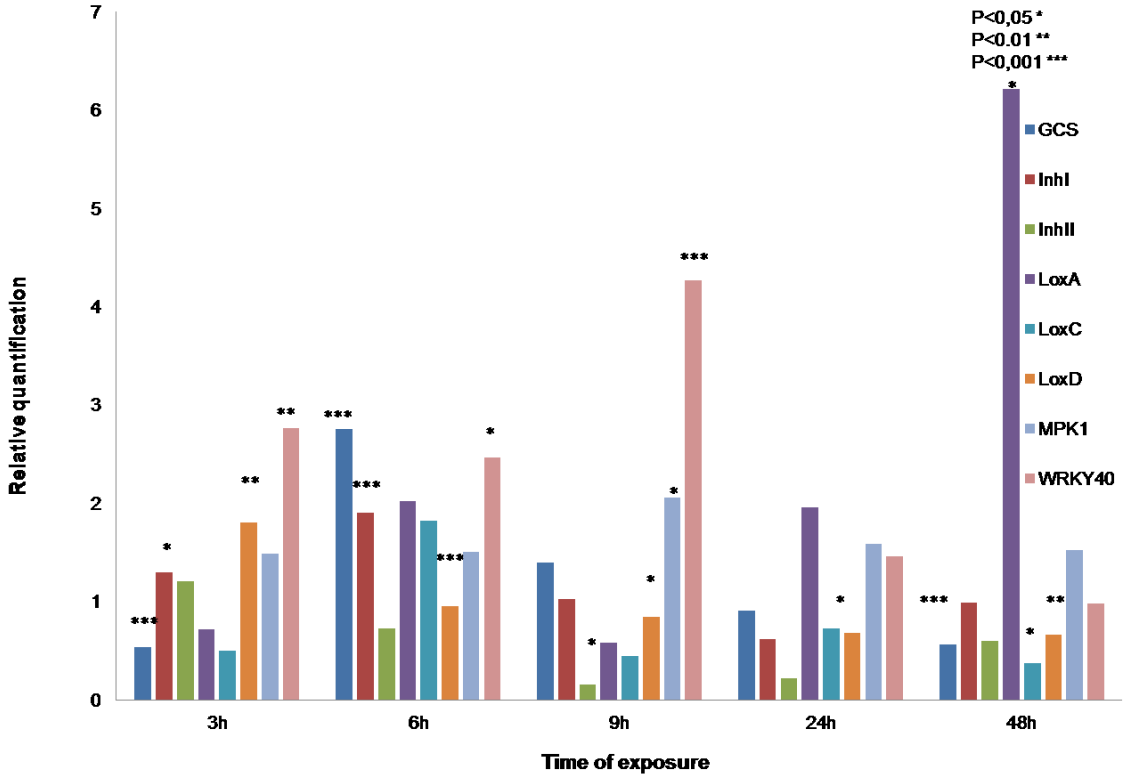


Figure 18: Relative Quantification of the genes expressed in the receiver plants R3 exposed to plants treated with the systemin peptide at different time points. The asterisks indicate statistical significance, Student's t-test (* p <0.05; ** p <0.01; *** p <0.001).

The differential regulation of gene expression starts after 3 hrs of exposure similarly to what observed in R2 plants. The majority of the selected genes resulted up-regulated after 6 hours of exposure. Interestingly, also in R3 plants *WRKY40* over-expression shows its maximum value after 9 hours of exposure. These observations demonstrated that Systemin foliar applications in source plants induce several defense related genes in neighbouring undamaged plants.

3.4 *Spodoptera littoralis* weight increase and survival rate: Induction of direct defense

In order to evaluate if the modified gene expression occurred in receiver plants exposed to the 3 different source plants were able to counteract insect infestation, bioassays were performed for the evaluation of *S. littoralis* larval weight and survival rate after feeding them on leaves of receivers plants.

3.4.1 Effect of the exposure to chewed plants source on direct defense against *S. littoralis* larvae

S. littoralis larvae were fed on leaf disks of tomato receiver plants. Larvae survival rates and weights, compared by Kaplan-Meier and log-rank test, did not show significant differences in comparison with controls (data not shown).

3.4.2 Effect of the exposure to transgenic plants overexpressing *Prosys* on survival and weight increase of *S. littoralis* larvae

The bioassay above described was also performed on R2 plants. These plants are known to release a quantitative and qualitative modified volatile blend. VOCs emitted by ProSys over-expressing plants are enriched in β-ocimene, α-pinene, β-myrcene/3-carene and limonene that affect the foraging behaviour of the parasitoid *A. ervi* (Corrado et al., 2007; Degenhardt et al., 2010). Starting by these previous observations, the aim of this experiment was to assess if the modified VOCs blend is effective in reducing larval growth and survival. Survival curves were compared as previously described. A significant difference between larvae feed on control leaves and larvae fed on R2 leaves were observed as shown in Figures 19 and 20. Larvae vitality and weight gain were strongly reduced after feeding on R2 plants demonstrating that the observed activation of defense related genes occurring in these plants after exposure to S2 plants is able to induce direct defenses able to interfere with insect larvae growth and vitality.

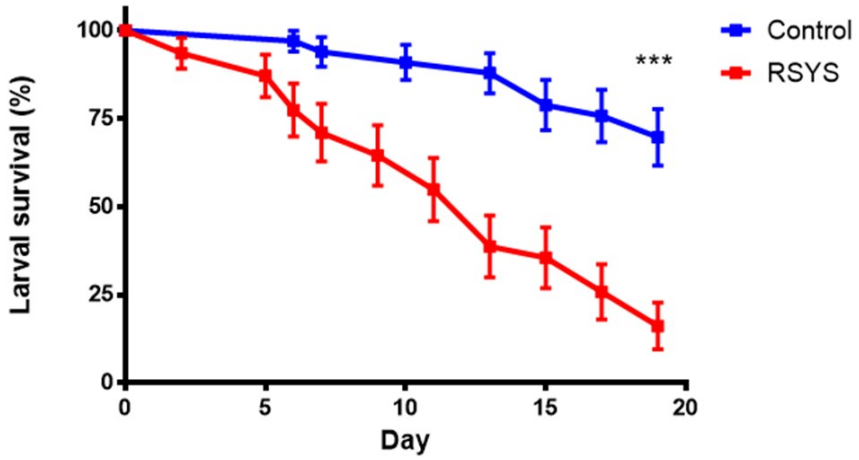


Figure 19: *S. littoralis* survival assay. Survival rate of larvae feed on plants exposed to transgenics overexpressing Prosystemin (RSYS) and control. Survival curves were compared using Kaplan-Meier and log-rank test (*** $p<0.0001$).

As shown in figure 20 a highly reduced larval weight was detected starting from day 5 of feeding. A very strong difference in weight is observed at 15 days of feeding, when the larvae reached the five instar, which is the stage in which the larvae eat a high amount of leaf tissue.

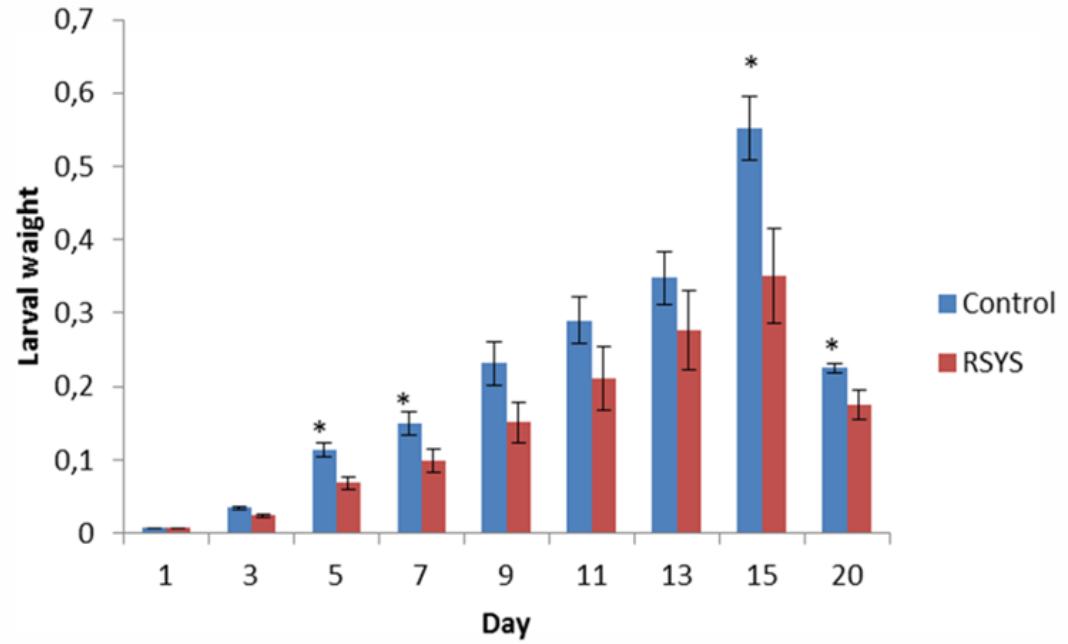


Figure 20: Weight increase of *S. littoralis* larvae fed on receiver plants exposed to plants overexpressing Prosystemin (RSYS) and to control plants. ***p<0.001; *p<0.05 (T-Student test).

3.4.3 Effect of the exposure to plants with foliar applications of Systemin on survival and weight increase of *S. littoralis* larvae

Also in this experiment, larvae survival and weight gain, following their feeding on R3 plants, show a remarkable decrease as shown in Figure 21 and 22.
These results demonstrated that, even in this case, the activation of defense related genes occurring in R3 plants is able to induce direct defenses able to interfere with insect larvae growth and vitality.

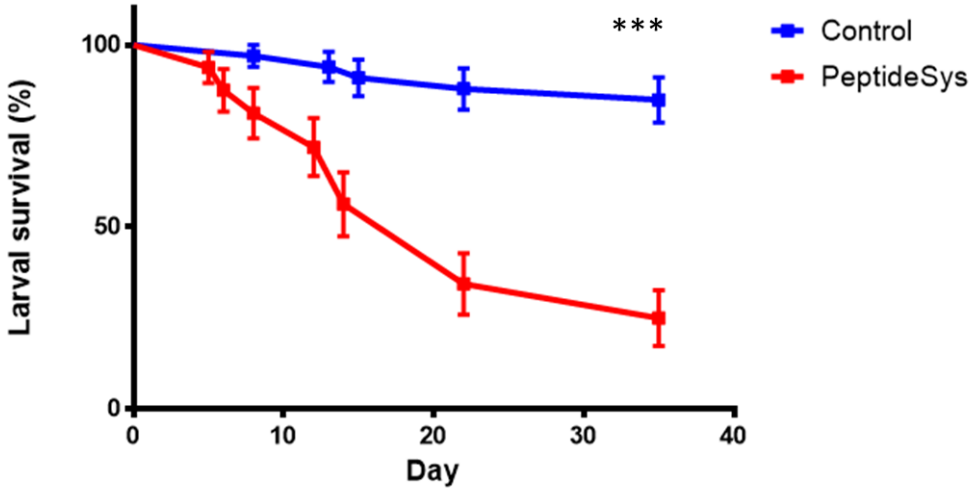


Figure 21: *S. littoralis* survival assay. Survival rate of larvae feed on plants exposed to source plants with peptide foliar application and control. Survival curves were compared using Kaplan-Meier and log-rank test (*** p<0.0001).

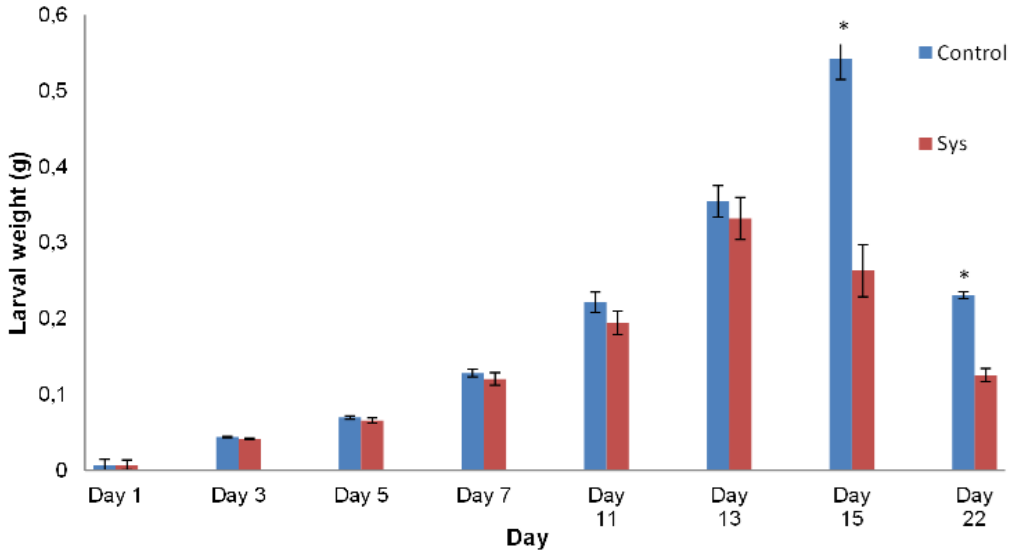
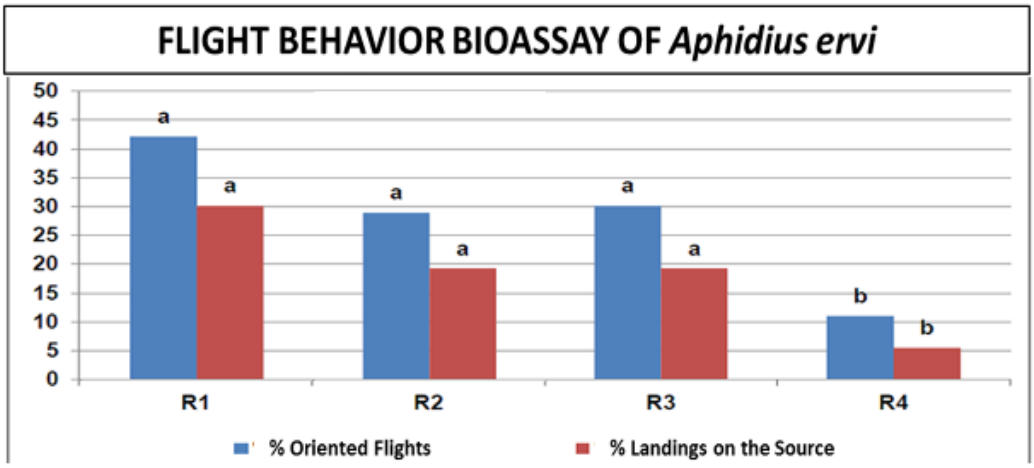


Figure 22: weight increase assay of *S. littoralis* larvae fed on receiver plants exposed to plants treated with peptide foliar application and to control plants. ***p<0.001; *p<0.05 (T-Student test).

3.5 Induction of indirect defenses in receiver plants

The observations of the induction of direct defenses following the different exposures, motivated a deeper investigation on the pre-alerted state of neighbour plants. Therefore it was investigated if the VOC blend emitted by the receiver plants were also able to attract natural enemies of herbivores. To this aim, a bioassay of attractiveness of receivers plants towards the *Aphidius aervi* parasitoid of the aphid *Macrosiphum euphorbiae* was performed. This assay was conducted in collaboration with the research group of Dr. Emilio Guerrieri of the Institute for Sustainable Plant Protection (IPSP-CNR). For this purpose, receiver plants exposed to the corresponding sources (Table 3) for 24h were tested in the wind tunnel. The behaviour of the parasitoids in terms of oriented flight and landing on the target, was registered. The obtained results are shown in figure 23.



Thesis	% Oriented Flights	% Landings on target
R1	42,169	30,120
R2	28,916	19,277
R3	30,120	19,277
R4	10,989	5,495

Figure 23: Attractiveness of receiver plants towards *Aphidius ervi*. R1: receiver plants exposed to plant chewed by *Spodoptera littoralis*. R2: receiver plants exposed to RSYS plant. R3: receiver plants exposed to plants treated with systemin peptide. R4: receiver plants exposed to untreated plant, (control). Letters a / b: statistical groups.

Receiver plants show higher attractiveness towards *Aphiudius ervi* compared to control plants (R4). It is well known that insect injured plants modify the VOCs blend making it more attractive to natural enemies of insect pests (Sasso et al., 2007; Ton et al., 2007). This phenomenon is one example of plant-insect communication or, communication with the third trophic level (Paré and Tumlinson, 1999; Wei, 2001; Arimura et al., 2001). There are several example in the scientific literature demonstrating that the ecological relationships of insect damaged plants include defense priming of neighbouring plants (Engelberth, 2004; Heil and Bueno, 2007; Frost et al., 2008). On the contrary, to our knowledge, the results obtained with transgenic and systemin treated plants, are new examples of plant-to-plant communication which lead to the induction of defense genes.

3.6 Qualitative and quantitative evaluation of VOCs from source and receiver plants

The different attractiveness towards the *Aphidius aervi*, parasitoid of the aphid *M. euphorbiae,* registered within the three experimental conditions described before, prompt to investigate the composition of volatile blends. This analysis was carried out in collaboration with Dr Emilio Guerrieri of the Institute for Sustainable Plant Protection (IPSP-CNR). Volatiles from source and receiver plants were collected by an airtight entrainment system immediately after the wind-tunnel bioassay and they were analyzed by gas chromatography and mass spectrometery (GC-MS).
VOCs profiles modifications were firstly analyzed in source plants. Larvae feeding effect on plant volatile blend have been widely reported (Mithofer et al., 2005; De Moraes et al., 2001; Paré et al., 1999) as well as modifications in VOCs release due to *ProSys* over-expression (Corrado et al., 2007). Chemical basis of the influence

exerted by Sys petide-treated plants on its neighbourhood were underlined through the VOCs identification. Quantitative and qualitative differences in volatile compounds emissions were registered for all source plants compared to the control (Table 5).

Table 5: VOCs analysis by GC-MS of source plants. S1: plant chewed by *Spodoptera littoralis;* S2: transgenic plant RSYS; S3: plants treated with systemin peptide S4: untreated plant (control). Mean values (pg g-1 fresh weight) ± Standard errors are shown for each volatile compounds released.

VOCs released	S1	S2	S3	S4
2,4-Dimethyl-1-heptene	10.2641 ± 1.6721	32.2671 ± 5.9058	13.8052 ± 2.2438	14.3609 ± 4.6234
Ethylbenzene	2.0897 ± 0.3364	5.8502 ± 1.7565	2.167 ± 0.5068	2.5535 ± 0.632
p-Xylene	6.006 ± 0.8627	12.8224 ± 4.959	6.1374 ± 1.3333	6.7338 ± 1.5734
Amyl acetate	0.3634 ± 0.0599	0.9497 ± 0.2427	0.4315 ± 0.0745	0.4522 ± 0.0984
1-heptanol	0.0676 ± 0.0676	3.439 ± 1.5398	0 ± 0	0 ± 0
1,4-dichlorobenzene	5.155 ± 0.8516	13.6842 ± 5.0644	4.4297 ± 1.0831	5.9634 ± 1.1346
β-Ocimene	0.0267 ± 0.0267	0.1742 ± 0.093	0.0982 ± 0.0546	0 ± 0
2-ethyl-1-hexanol	7.7732 ± 1.7476	15.5146 ± 5.4583	8.1939 ± 1.7625	6.6806 ± 1.2868
acetophenone	0.9984 ± 0.1683	3.0498 ± 1.0509	1.1253 ± 0.2282	1.2085 ± 0.2162
p-tolualdehyde	1.8222 ± 0.2561	6.5363 ± 1.9133	2.4507 ± 0.3972	2.4026 ± 0.6195
naphthalene	23.6009 ± 3.6453	66.2025 ± 23.1726	27.0323 ± 4.8271	27.8429 ± 5.1834
1-dodecene	2.4444 ± 0.4501	7.5973 ± 2.8547	3.0484 ± 0.649	3.029 ± 0.5727
Benzaldehyde, 2,4-dimethyl-	0.4636 ± 0.0644	1.5281 ± 0.5859	0.515 ± 0.098	0.5411 ± 0.0924
4-vinylphenol	0.5341 ± 0.2177	0.198 ± 0.198	0.7996 ± 0.2121	0.8253 ± 0.1909
benzothiazole	1.5791 ± 0.7088	4.1273 ± 1.6013	1.1762 ± 0.2791	1.0332 ± 0.1853
alfa pinene	0.3176 ± 0.055	0.8174 ± 0.2748	0.3387 ± 0.0748	0.3862 ± 0.0825
limonene	0.2909 ± 0.0474	0.7455 ± 0.2702	0.3093 ± 0.0638	0.3613 ± 0.0695
linalool	0.5132 ± 0.0833	1.5489 ± 0.6021	0.6151 ± 0.1178	0.6192 ± 0.1164

Among sources, transgenic plants constitutively expressing *ProSys* were predominant in VOCs release. In concordance with Corrado and co-workers (2007) results, β-ocimene, limonene and α-pinene were more abundant in transgenic plants

compared to the control (table 5). These compounds are monoterpenes, the most abundant group among volatile terpenoids fastly induced following herbivory (Mumm et al., 2008).
Other abundant compounds are benzenoids as p-Xylene, 1,4-dichlorobenzene, Benzaldehyde,2,4-dimethyl, Naphthalene and Benzothiazole. Reports of the synthesis and/or emission of benzenoid esters from leaves are very few. They come from shikimic acid pathway in which phenylpropanoids and other defensive compounds are produced. Emission of methylsalicylate (MeSA), and occasionally of methylbenzoate (MeBA), from *Arabidopsis thaliana* leaves was detected following the application of some kind of both biotic and abiotic stresses to the plant (Chen et al., 2003). Another compound released in large amount by transgenic plants is for example the alkene 1-dodecene, recently associated to plant competition for light (Kegge et al., 2013) and the host choice by *Aphis gossypii* in *Capsicum spp* (Da Costa et al., 2011). Plant phenols as acetophenone have been associated to resistance to herbivory (Harbore, 1993; Hammerschmidt, 2005).
The other two types of plant sources are less influenced in volatile blend compared to transgenic plants. Interestingly, β-ocimene release is more abundant in Sys-treated plants and in transgenic plants compared to the control, while is absent in chewed-plant release indicating that its release could be specifically influenced by systemin (Table 5). The terpenoid 1-heptanol is emitted by chewed and transgenic plants while is absent in VOCs of S3 and S4. This compound has been identified in the volatile blends emitted by *Medicago truncatula* upon *Spodoptera littoralis* and *Tetranychus urticae* infestations indicating its involvement in responses to different herbivory stiles (Leitner et al., 2005). This finding is in agreement with the oserved tolerance of ProSys over-expressing plants to phytophagous and phloem feeders (Coppola et al., 2014).
Once demonstrated VOCs alterations in source plant, the aim of my research activity focused on the ability of these source plants to induce modifications in volatile blends of receiver plants. To this purpose, VOCs were collected and analyzed as for source plants. Table 6 lists the differentially compounds released from receiver plants compared to the control.

Table 6: VOCs analysis by GC-MS of receiver plants. R1: plant exposed to plants chewed by *Spodoptera littoralis;* R2: plant exposed to transgenic plant RSYS; R3: plant exposed to systemin-treated plant; R4: plant exposed to untreated plant (control). Mean values (pg g-1 fresh weight) ± Standard errors are shown for each volatile compounds released.

VOCs released	R1	R2	R3	R4
2,4-Dimethyl-1-heptene	12.1636 ± 2.2963	13.8323 ± 2.597	21.1185 ± 4.4608	13.3111 ± 3.3908
Ethylbenzene	2.3475 ± 0.4796	2.3484 ± 0.3575	2.3097 ± 0.3994	2.7257 ± 0.6377
p-Xylene	6.998 ± 1.2153	6.624 ± 1.2566	8.6292 ± 1.4987	8.2506 ± 2.1974
Amyl acetate	0.5146 ± 0.14	0.4247 ± 0.0796	0.489 ± 0.0766	0.4807 ± 0.1049
1-heptanol	0.9293 ± 0.3244	1.1244 ± 0.3817	1.0527 ± 0.4114	1.3657 ± 0.4278

1,4-dichlorobenzene	6.0373 ± 1.2119	6.136 ± 1.177	7.667 ± 1.5971	7.622 ± 2.2909
β-Ocimene	0.1609 ± 0.0959	0.0489 ± 0.0443	0.2265 ± 0.1035	0 ± 0
2-ethyl-1-hexanol	7.1676 ± 1.4032	7.1111 ± 1.4065	8.5359 ± 1.6822	9.9573 ± 3.0689
acetophenone	1.2966 ± 0.1957	0.9845 ± 0.1998	1.438 ± 0.4395	1.3795 ± 0.387
p-tolualdehyde	2.3816 ± 0.3119	1.7538 ± 0.4484	3.7601 ± 0.9613	2.706 ± 0.7754
naphthalene	27.2688 ± 4.7471	26.2957 ± 4.6487	37.4862 ± 6.8839	31.9383 ± 9.1619
1-dodecene	3.1478 ± 0.6093	3.1018 ± 0.6402	4.1405 ± 0.7282	3.6768 ± 1.2184
Benzaldehyde, 2,4-dimethyl-	0.6024 ± 0.1355	0.4959 ± 0.094	0.7173 ± 0.1489	0.6487 ± 0.1646
4-vinylphenol	0.1929 ± 0.0677	0.0925 ± 0.0925	0.0297 ± 0.028	0.0226 ± 0.0226
benzothiazole	1.517 ± 0.3732	0.7183 ± 0.1567	1.3984 ± 0.2395	1.2738 ± 0.3447
alfa pinene	0.4042 ± 0.0983	0.4061 ± 0.0754	0.4563 ± 0.0895	0.4701 ± 0.1301
limonene	0.3408 ± 0.0709	0.3464 ± 0.065	0.4216 ± 0.0817	0.3879 ± 0.1136
linalool	0.651 ± 0.1388	0.6061 ± 0.1115	0.785 ± 0.1143	0.7579 ± 0.2429

β-ocimene is the unique identified compound exclusively released by R1, R2 and R3 plants and totally absent in the control (table 6). Frost workgroup (2008) observed stronger emissions of β-ocimene from leaves with prior exposure to GLVs in poplar. Its presence was also detected in volatile bouquet released by undamaged poplar plant exposed to *Lymantria dispar*-damaged plants (Frost et al., 2008). In addition to (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT) and (*E*,*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT), β-ocimene was found to elicit the expression of Lypoxigenase 3 (LOX), Phenylalanine ammonia lyase (PAL) and farnesyl pyrophospate synthetase (FPS) genes in uninfested leaves (Arimura et al., 2000).
2,4-Dimethyl-1-heptene is released by all receiver plants with a higher amount by plants exposed to Sys-treated plants. Among compounds released by source plants, no one has been specifically associated to Sys treatment (table 5). Since in the initial steps of alkene synthesis, mevalonic acid is converted in isopentenylpyrophosphate, known to be a terpenoid precursor, amounts and relative proportions of compounds present in the volatile blend of S3 plants could prompt alkene synthesis in R3 plant.
Recently, 2,4-Dimethyl-1-heptene has been found in the volatile mixture associated to the host preference by the parasitoid *Microplitis mediator* in *Brassica oleracea* plants (Weldegergis et al., 2015). This observation are consistent with the high attractiveness towards *A. ervi* registered in R3 plants (par 3.5).

3.7 Transcriptomic reprogramming of plants exposed to source plants treated with systemin peptide

In order to identify a larger number of molecular functions active in plant to plant communications, which could result in the observed increase of direct and indirect defenses in R3 plants, (exposed to plants treated with Systemin), transcriptome sequencing was carried out.
Total purified RNA, extracted from 3 biological replicates both from untreated (C1, C2 and C4) and R3 plants (P1, P2 and P4), was converted to cDNA and then sequenced by Illumina HiSeq1500 (external service). The raw data for each sample consists of a long list of short sequences (reads) with associated quality scores (*fastq* format). The quality of the sequences was evaluated with the FastQC software. Results are shown in Figure 23. The y axis shows the quality values divided into three distinct parts, by different colours. The green, the orange and the red corresponding to high, average and low quality base calling, respectively per position in the read (Figure 24).

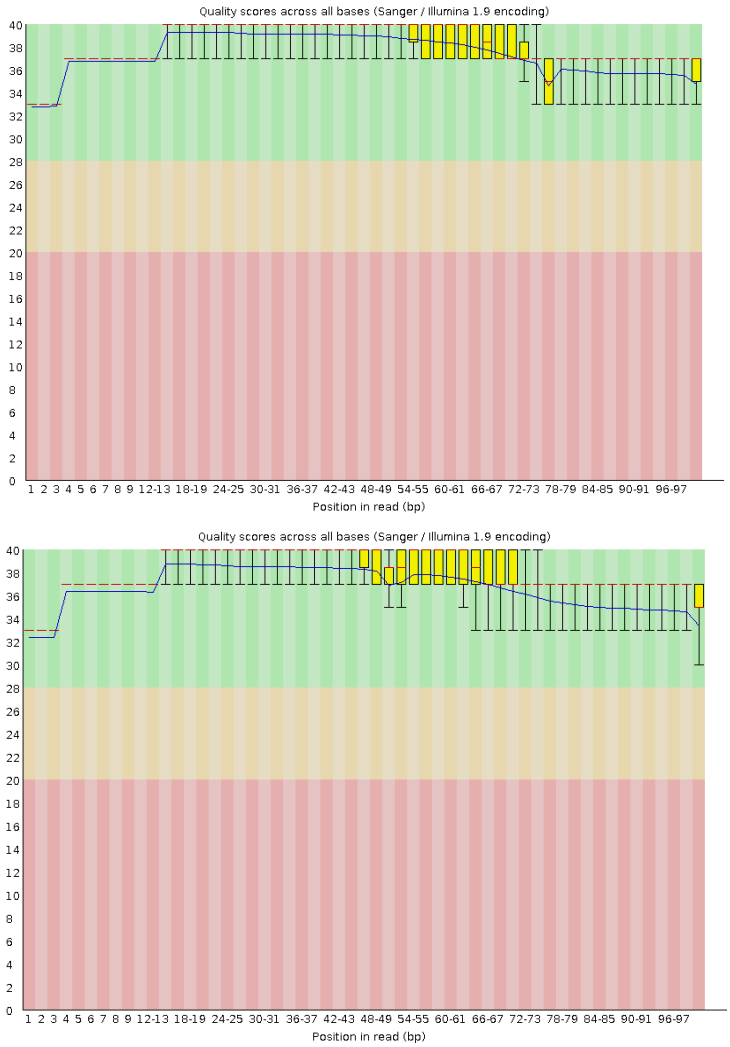


Figure 24: FastQC analysis result for sample C1, for paired ends R1 and R2

Trimmomatic and Fastqc softwares (TrimGalore package (http://www.bioinformatics.babraham.ac.uk/projects/trim_galore/) were used to eliminate low quality regions and filter out reads shorter than 30nt. The results are shown in figure 25.

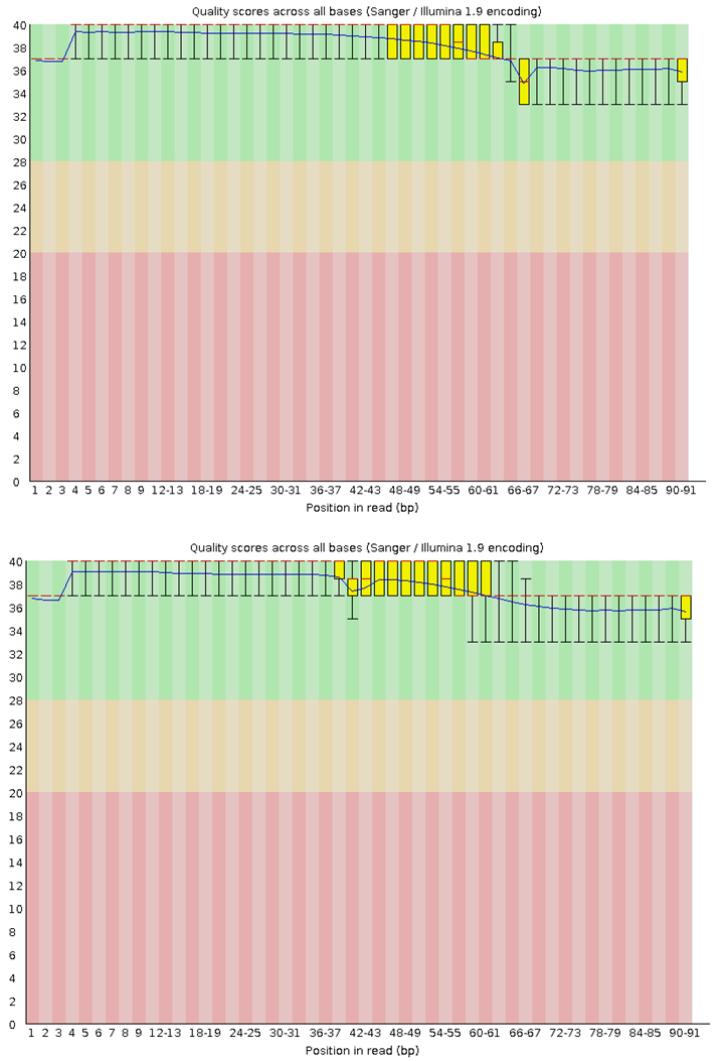


Figure 25: FastQC analysis result for sample C1, R1 and R2 after Trimming

The high quality reads obtained after the cleaning steps, were mapped to the tomato reference genome (http://solgenomics.net/organism/Solanum_lycopersicum/genome) which is composed of 12 chromosomes for a total of 950Mbp containing 34727 genes. 19662 genes, 56.6% of total, are annotated with GO terms. The mapped reads were quantified with the feature Counts program (Robinson et al., 2010).
After data processing, further filtering was performed through the HTS Filter software, that reduces the number of highly variable or poorly expressed genes. The total number of filtered genes were 21351.
The Principal Component Analysis (PCA, Figure 26) of filtered and normalized data allowed the identification of two replicas, C4 and P1 that did not comply with the respective other replicas and therefore were eliminated.

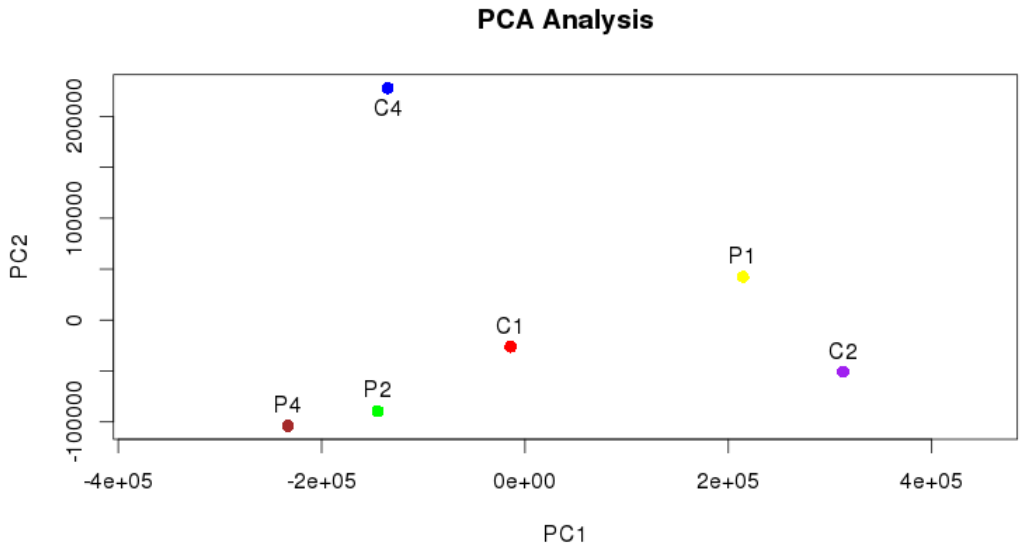


Figure 26: PCA of filtered gene with HTS Filter

3.7.1 EdgeR analysis

The statistical analysis was performed by EdgeR. The dispersion function was calculated by three steps:
1- calculation of total dispersion of the experiment;
2- dispersion calculation for groups of genes, whose common denominator is an average value of similar expression;
3- dispersion calculation for every single gene.
The recommended test was a General Linear Model (GLM), using a linear regression as a model.
The resulting differentially expressed genes and their FDR, indicating statistical significance, are reported by a BARPLOT with differentially and not differentially expressed genes (Figure 27).

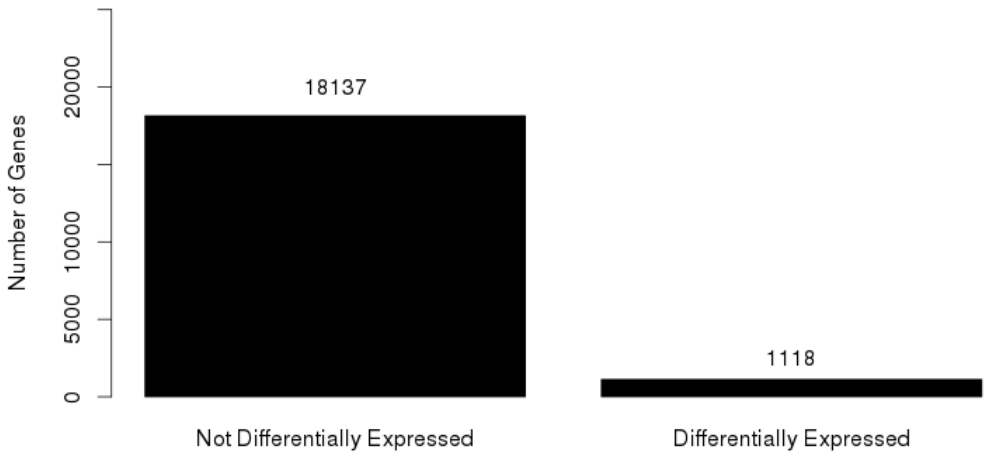


Figure 27: BarPlot of differentially and not differentially expressed genes after EdgeR analysis

A total number of 1118 differentially expressed genes was identified. Among them, 537 genes were up-regulated while 581 were down-regulated (Figure 28).

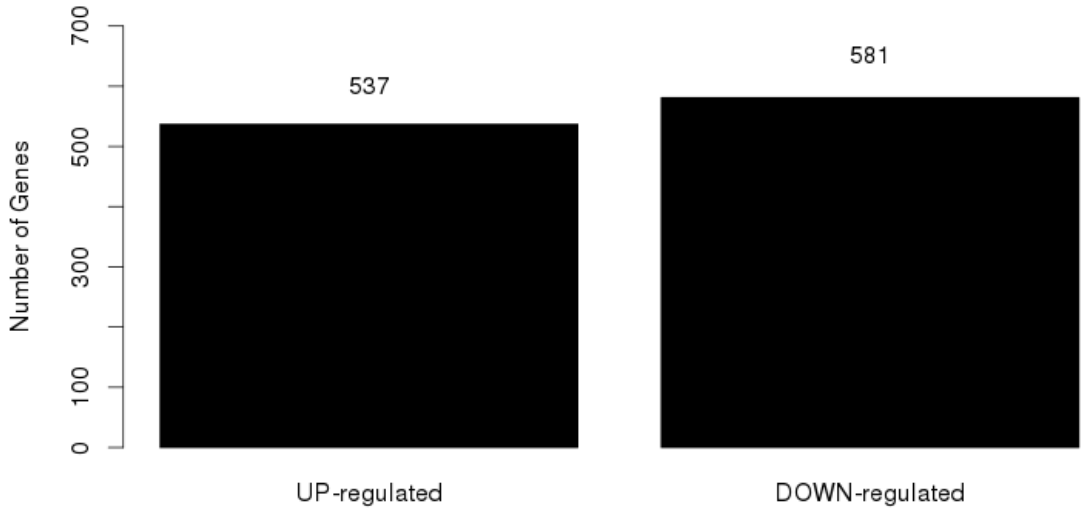


Figure 28: BarPlot of up and down-regulated genes

A graph representing in red up-regulated genes and in green down-regulated ones is also shown in Figure 29. The MAPlot presents on the x axis the medium value of expression for all the analized genes and on y axis the fold change.

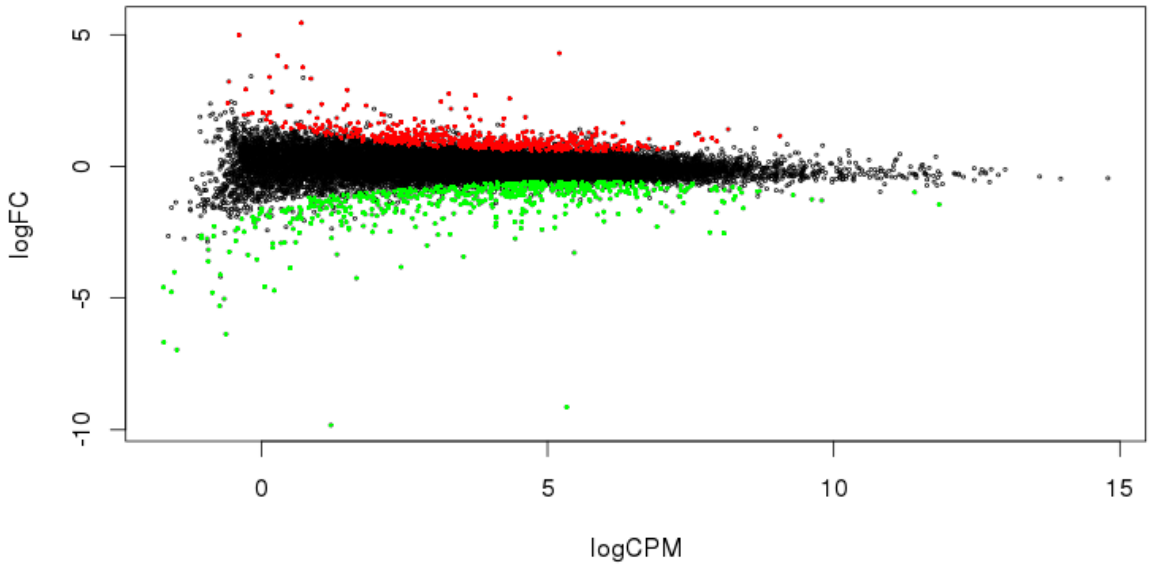


Figure 29: MAPlot of differentially expressed genes in red are shown UP genes, in green DOWN gene

Similar results were obtained through the NOISeq analysis (not shown).

3.7.2 Functional annotation of differentially expressed genes: Gene Ontology and enrichment analysis (GOEA)

The 1118 differentially expressed genes (DEG) were functionally annotated with AgriGO (Du et al., 2010) and Blast2GO software (Conesa et al., 2005), taking as

reference the annotation of the tomato genome. GO categories and enrichment scores of up and down-regulated genes are shown respectively in Figures 30 and 31 while functional annotations of selected genes of both classes, is shown in tables 6 and 7, (all the differentilly expressed genes are listed in table 1 and 2 in appendix).
Among the most represented ontological category of up regulated genes there are enzymatic activities, like kinase activity involved in many signal transduction pathways, including defense signalling pathway (Meng et al., 2013). Protein kinases play a central role in signalling during pathogen recognition and the subsequent activation of plant defence mechanisms. Moreover, MAPKs are essential components of the systemin signaling pathway required for successful plant defense against herbivorous insects (Kandoth et al., 2007). Plant kinases have been reported to be induced by oral secretions of herbivorous insects in different species (Wu et al., 2007; Yan et al., 2007) but also by abiotic stresses (Sinha et al., 2011), mechanical wounding and green leaf volatiles (Dombrowski et al., 2011). The results here shown demonstrated that MAPK are also involved in defense priming in tomato plants.
Receptor-like kinases (RLKs), also up-regulated, is an important class of sentinels acting in plant defense responses. Recent work has highlighted that, both elicitor perception in the plant innate immune response and R-gene modulated pathogen specific responses, are mediated in many cases by plant RLKs (Zeng et al. 2006). Interestingly the results here shown indicated that receptor kinase activities are also involved in tomato defense priming possibly contributing to the perception of the airborn signal emitted by Systemin treated plants or by plants damaged by larvae.
The great increse in catalytic and tranferase activity registered in R3 plants (Figure 30), indicate that in these plants several chemical reactions increase their rates following the exposure to S3 plants in order to produce both primary and secondary metabolites that cooperate in plant-to-plant communication and the activation of defense responses.

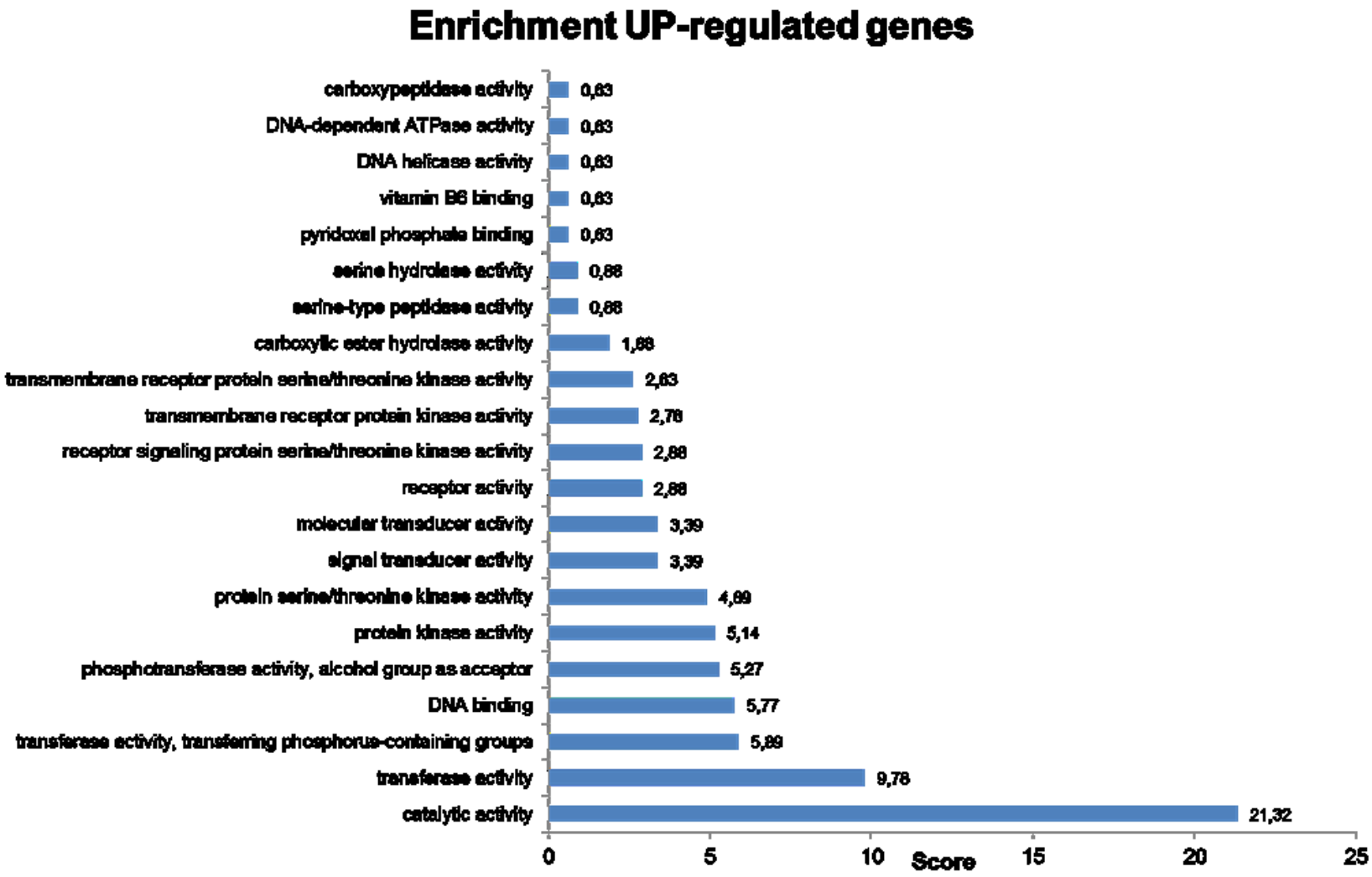


Figure 30: GO categories and enrichment score of up regulated genes

Several up-regulated genes (Table 7) are both early and late defense genes. Among the encoded proteins of the former class, beside Protein Kinases already considered, there are Knotted-like homeobox protein, Calmodulin, Ap2-ethylene-responsive transcription factor and Gdsl esterase lipase.
The homeobox is a semi-conserved sequence motif of about 180 base pair encoding 60 amino acid sequences, highly conserved among animal, fungal, and plant proteins and referred as the homeodomain. Generally, homeodomain are transcription factors that control many developmental processes (Lawrence and Morata,1994). In plants, homeobox genes are involved in a variety of functions, including response to stress. Two major classes of homeodomain-encoding genes have been identified in plants: the homeodomain class represented by KNOTTED1 (Vollbrecht et al., 1991) and the family of HD-Zip proteins (Schena and Davis, 1992). The former encode Knotted1-proteins (KNOX) proposed to be involved in the regulation of cytokinin (CK) biosynthesis as the production of active CKs is significantly increased in KNOX overproducing plants (Sakamoto et al., 2006). Recently, investigation of the hormonal interplay occurring in plant immunity proved that CKs promotes defense against various plant pathogens, thus belonging to the plant defense network (Choi et al., 2011). The presented results suggest a possible increase in CK promoting a defense condition.
Calmodulins (CaMs) are calcium sensor proteins which play a crucial role in cellular signaling cascades through the regulation of numerous target proteins. During plant defense responses, the increase in calcium concentration is a fundamental early event. Previously identified elements of plant defense signaling pathways include diverse CaMs, CMLs and CaM-binding proteins (Heo et al., 1999).
The upregulation of *Ap2-ethylene-responsive transcription factor* is likely to be involved in the modulation of JA and ET pathways simultaneously (Pieterse et al. 2009), while Gdsl esterase lipase, hydrolytic enzymes with multifunctional properties, are involved in defense against *Alternaria brassicicola* and *Erwinia carotovora* (Lee et al., 2009).
Among the encoded proteins of the latter class there are Peroxidase, Proteinase inhibitor and Polyphenol oxidase all known to be involved in plant defense mechanisms (Walling, 2000).
Taken toghether these data indicate that receiver plants underwent a modulation of transcription in the direction of defense promotion, starting from early signals to defense effectors.

Table 7: List of up regulated genes with logFC > 1.5. Genes description were obtained according to Blast2GO and AgriGO annotations

Locus	logFC	PValue	Blast2GO annotation	AgriGO annotation
Solyc04g077210.2	3,77	1,52E-08	Homeobox protein knotted-1	Knotted-like homeobox protein
Solyc01g094380.2	2,93	9,37E-05	O-glucosyltransferase rumi homolog	Glycosyltransferase CAZy family GT90 (Fragment)
Solyc03g119820.1	2,41	1,06E-03	Oleosin 1	Oleosin Bn-V
Solyc02g078690.1	2,31	6,02E-07	Serine carboxypeptidase-like 31	Serine carboxypeptidase K10B2.2
Solyc04g014260.1	2,31	4,46E-05	Zinc-finger homeodomain protein 1	Zinc finger-homeodomain protein 1 (Fragment)
Solyc11g010710.1	2,31	9,10E-05	Ap2-like ethylene-responsive transcription factor ail6	AP2-like ethylene-responsive transcription factor
Solyc02g089170.2	2,04	3,98E-04	Alpha- -glucan-protein synthase	Alpha-1 4-glucan-protein synthase
Solyc01g007080.2	2,02	1,51E-03	Aluminum-activated malate transporter 8	Aluminum-activated malate transporter (Fragment)
Solyc05g046020.2	1,97	3,32E-08	Peroxidase 3	Peroxidase
Solyc03g020030.2	1,96	1,89E-05	Proteinase inhibitor type-2 cevi57	Proteinase inhibitor II
Solyc04g074900.2	1,96	2,35E-03	40s ribosomal protein s21	40S ribosomal protein
Solyc04g049920.2	1,94	5,51E-04	RNA-binding protein 38	RNA binding protein
Solyc08g082630.2	1,88	4,96E-10	Auxin response factor 9	Auxin response factor 9
Solyc02g089620.2	1,88	4,36E-09	Proline dehydrogenase mitochondrial	Proline dehydrogenase
Solyc11g013220.1	1,84	3,01E-05	C2h2-like zinc finger protein	Os04g0690100 protein (Fragment)
Solyc02g069280.2	1,78	1,98E-03	Protein argonaute 2	Argonaute 1
Solyc03g005910.2	1,73	4,66E-05	Gdsl esterase lipase	GDSL esterase/lipase
Solyc07g041640.2	1,70	1,10E-04	Growth-regulating factor 1	Growth-regulating factor 1
Solyc04g074340.2	1,68	1,96E-03	7-deoxyloganetin glucosyltransferase	UDP-glucuronosyltransferase
Solyc01g103500.2	1,67	5,80E-04	Extended synaptotagmin-3	Unknown Protein
Solyc11g042880.1	1,66	3,28E-05	Predicted: uncharacterized protein LOC101261986	Harpin-induced protein

Solyc06g053870.2	1,66	1,25E-06	3-ketoacyl- synthase 19	Fatty acid elongase 3-ketoacyl-CoA synthase
Solyc08g074620.1	1,65	8,78E-16	Polyphenol oxidase	Polyphenol oxidase
Solyc03g115120.1	1,65	1,72E-07	DNAj homolog subfamily c member 21	Chaperone protein dnaJ
Solyc02g030460.2	1,64	4,53E-04	Methyl- -binding protein 2	Sh4 homologue protein
Solyc07g055180.2	1,61	8,12E-05	Serine threonine-protein kinase cdl1	Receptor protein kinase-like protein Serine/threonine protein kinase
Solyc10g007800.2	1,60	9,49E-04	Protodermal factor 1	Meiosis 5
Solyc10g087030.1	1,58	3,15E-04	Premnaspirodiene oxygenase	cytochrome P450
Solyc04g078460.2	1,58	7,24E-04	Probable isoaspartyl peptidase l-asparaginase 2	N(4)-(Beta-N-acetylglucosaminyl)-L-asparaginase Peptidase
Solyc00g138060.2	1,56	9,87E-04	Unknown Protein	2-oxoglutarate-dependent dioxygenase
Solyc08g083240.2	1,56	5,76E-08	Protein iq-domain 1	Calmodulin-binding protein
Solyc04g050570.2	1,56	9,79E-08	Gdsl esterase lipase	GDSL esterase/lipase
Solyc10g048190.1	1,55	1,46E-04	Thymocyte nuclear protein 1	Ubiquinol-Cytochrome c reductase iron-sulfur subunit
Solyc11g011310.1	1,53	8,24E-05	Probable rhamnogalacturonate lyase b	Rhamnogalacturonate lyase
Solyc10g074440.1	1,51	7,74E-10	Endochitinase	Endochitinase
Solyc03g122360.2	1,51	1,29E-04	Cytochrome p450 71a1	Cytochrome P450
Solyc01g089910.2	1,50	2,65E-03	Flotillin-like protein 6	Flotillin domain protein

In order to highlight the contribution of DEG in different metabolic pathways, KEGG analysis was carried out. Differentially expressed genes, are involved in phenylpropanoid biosynthesis and arginine and proline biosynthesis. Figure 31 showed phenylpropanoid biosynthesis pathways were red box represent up-regulated proteins

The phenylpropanoid biosynthesis produces a lot of compound with strong anti-microbial and anti-fungal activities (Dixon et al., 2002); as shown in figure 31 the activity of several enzymes involved in this pathways is induced. The up-regulation of 4 genes operating in final steps of the biosynthesis of lignin components most likely results in a variation of the strength and stiffness of the cell wall of R3 plants, aimed at reducing host invasion.

Figure 32 shows arginine and proline biosynthesis in which genes coding for enzymes at the beginning of the pathway are regulated by priming conditions.

The *Profilin* gene (Solyc12g044630.1) was up-regulated in this pathway: profiling binds to actin and affects the structure of the cytoskeleton. At high concentrations, profilin prevents the polymerization of actin, whereas it enhances it at low concentrations. By binding to C2 phosphatidylinositol-4,5-bisphosphate (PIP2), it inhibits the formation of IP3, cellular second messengers that induce changes of cytosolic Ca2+ concentration, therefore beeing a regulator of transmembrane signalling (Kudla 2010).

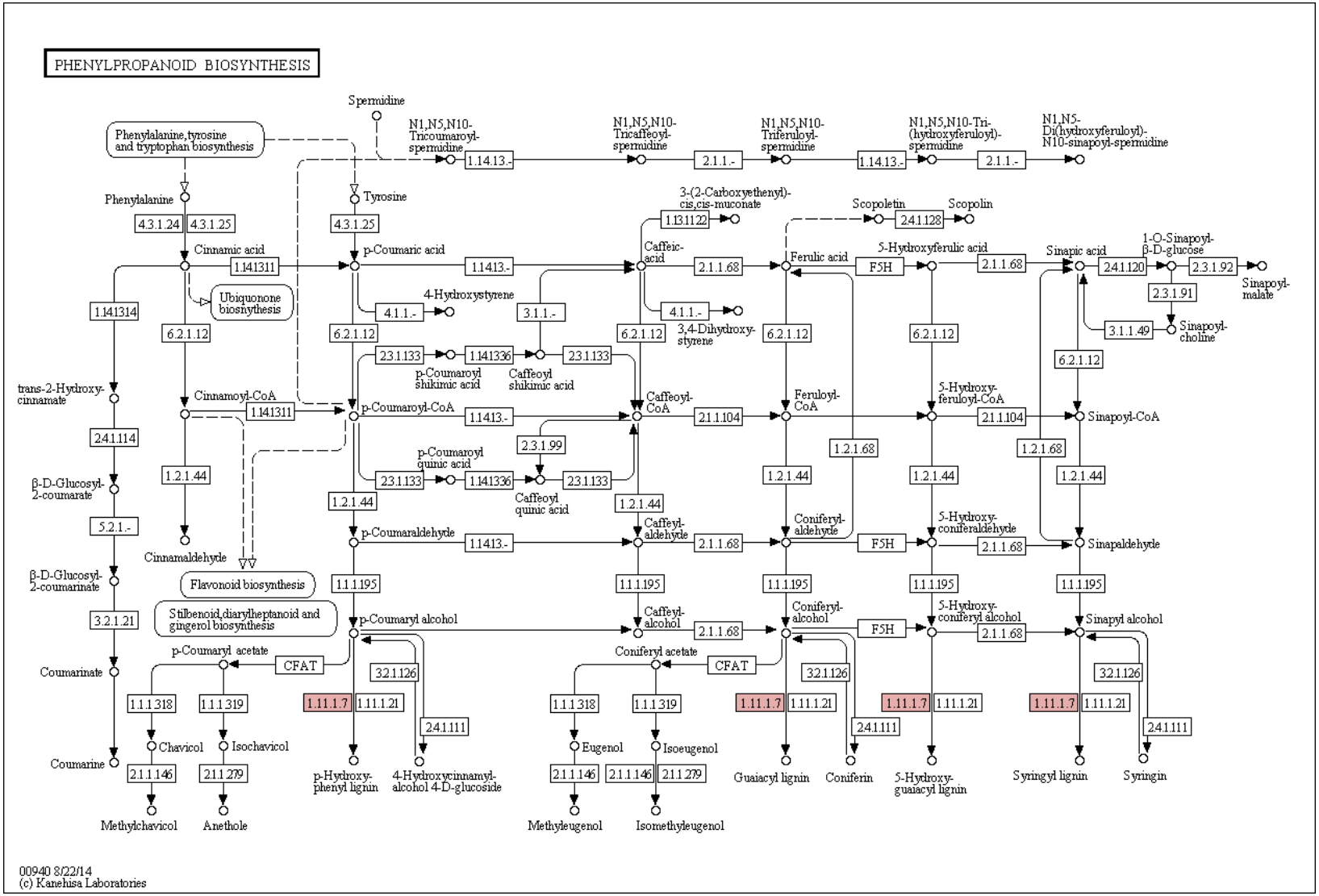


Figure 31: the figure displays the phenylpropanoid pathway. Enzymes whose expression is regulated by the exposition to Sys-trated plants are indicated in red

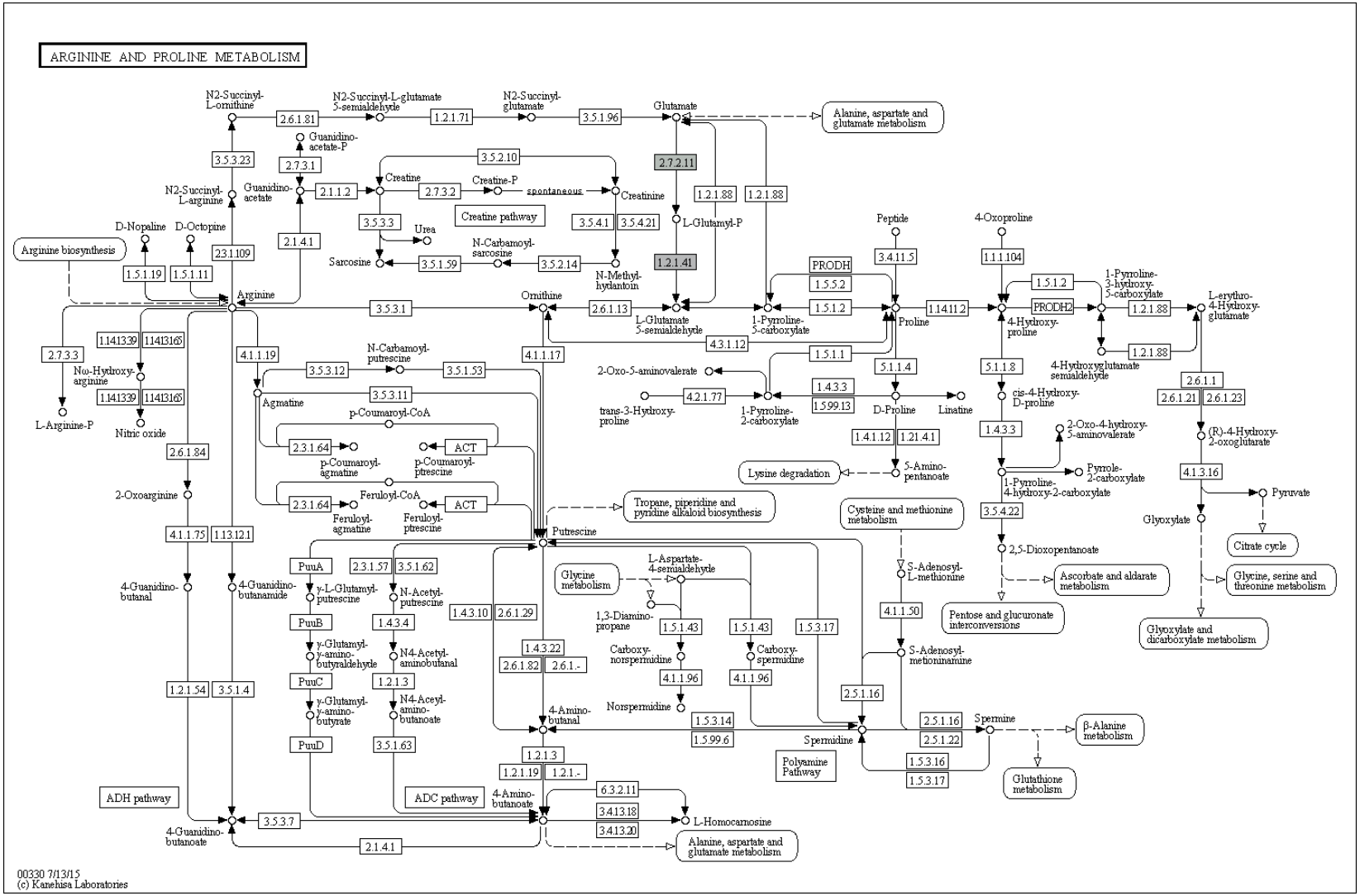


Figure 32: the image displays the arginine and proline metabolism. Enzymes whose expression is regulated by the exposition to Sys-trated plants are indicated in gray

Table 8 lists the down regulated genes with logFC greater than -2 (all down-regulated genes are listed in supplementary table 2 in appendix).
The most represented ontological categories of down regulated genes (figure 33) are enzymatic activities and metabolic process that take part in many signal transduction pathways, in which phosphate ion transmembrane transporter activity and cell wall macromolecule metabolic process are found.
The enrichment analysis of down-regulated genes indicate a modulation of signal transduction with cellular homeostasis and a lot of transported activity.

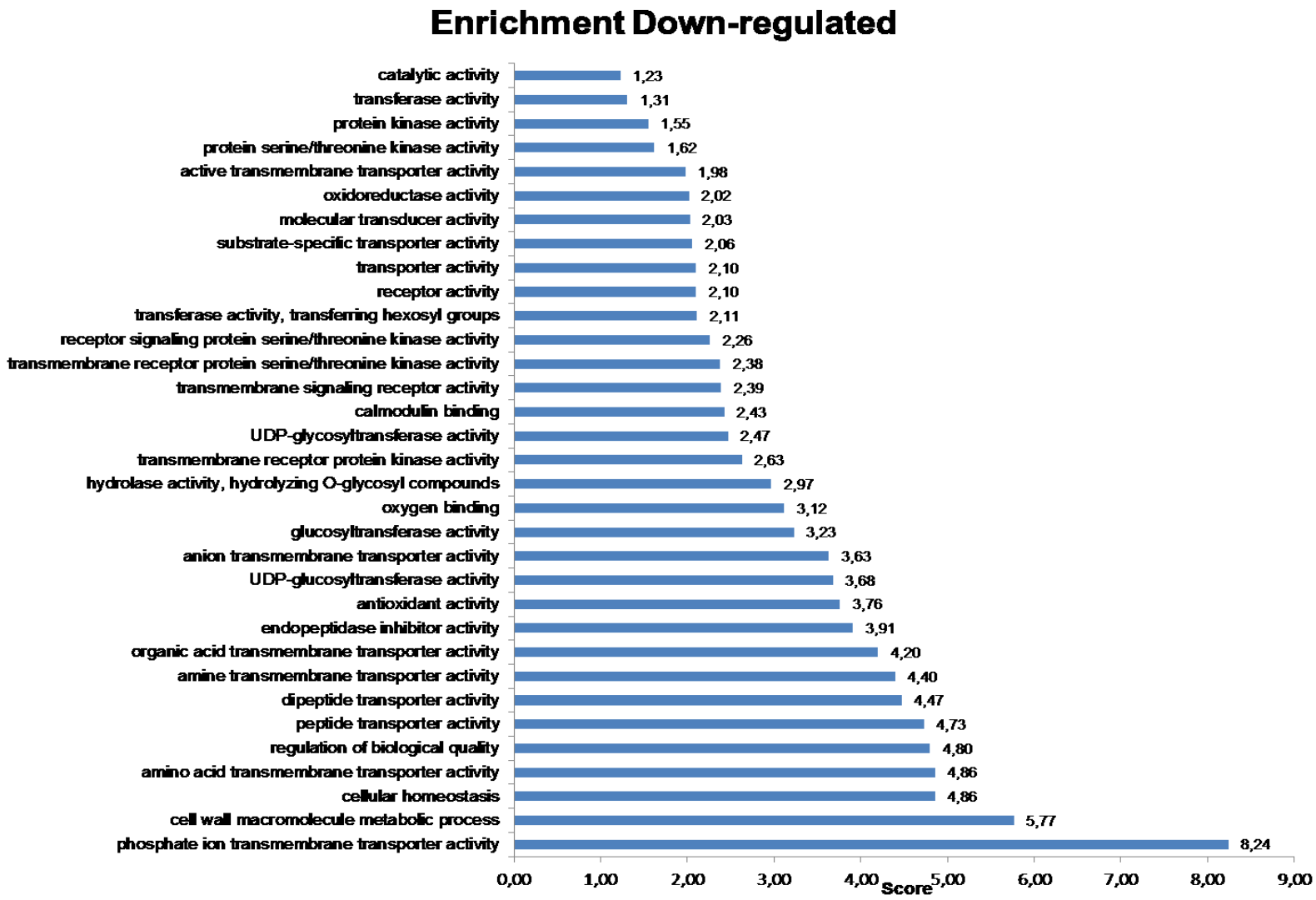


Figure 33: GO categories and enrichment score of down regulated gene

Among the down genes (Table 9) there are some that are involved in basic processes involved in plant development, such as Auxin-responsive protein, NAC domain transcription factor, Glutaredoxin, Phospholipase D, but also genes involved in defense against pathogen like Pathogenesis related protein PR-1, Osmotin, Laccase, Endochitinase and Ethylene-responsive transcription factor. The down regulation of the former group can be possibly explained considering that the defense alert received by R3 plants switch the metabolic activity from basal physiological processes towards defense responses or defense response preparation. Similarly it is possible to speculate that the down regulation of the latter group of gene, mainly involved in resistance to pathogenes, are not required following the aerial signal received. A deeper investigation of these aspect is necessary for a better clarification of these observations.

Table 8: List of down regulated genes with logFC >-2. Genes description were obtained according to Blast2GO and AgriGO annotations

Locus	logFC	PValue	Blast2GO Annotation	AgriGO annotation
Solyc04g052890.1	-6,68	7,83E-05	Auxin-induced protein 6b	Auxin-responsive protein
Solyc09g018200.1	-4,58	1,02E-03	Transcription repressor ofp1	Plant-specific domain TIGR01568 family protein
Solyc02g061780.2	-3,82	1,43E-25	NAC domain-containing protein 94	NAC domain transcription factor
Solyc04g011790.1	-3,59	7,63E-06	Monothiol glutaredoxin-s1	Glutaredoxin
Solyc09g008750.1	-3,53	9,44E-09	VQ motif-containing protein 29	Unknown Protein
Solyc02g079480.1	-3,35	1,31E-07	Tetrahydrocannabinolic acid synthase	FAD-binding domain-containing protein
Solyc05g052670.1	-3,00	2,81E-19	Uncharacterized acetyltransferase	N-hydroxycinnamoyl/benzoyltransferase 1
Solyc06g051860.1	-2,92	6,22E-07	Inorganic phosphate transporter 1-11	Inorganic phosphate transporter 6
Solyc03g116620.2	-2,82	1,73E-04	Phospholipase d alpha 1	Phospholipase D
Solyc09g007010.1	-2,74	2,62E-35	Pathogenesis-related leaf protein 4	Pathogenesis related protein PR-1
Solyc12g094610.1	-2,73	2,93E-04	U-box domain-containing protein 15	U-box domain-containing protein 15
Solyc03g033750.1	-2,65	1,45E-04	Probable mitochondrial chaperone bcs1-a	BCS1 protein-like protein
Solyc08g080640.1	-2,58	6,39E-19	Osmotin-like protein	Osmotin-like protein (Fragment)
Solyc08g080650.1	-2,53	2,63E-25	Osmotin-like protein	Osmotin-like protein (Fragment)
Solyc00g174340.1	-2,51	5,88E-27	Unknown Protein	Pathogenesis-related protein 1b
Solyc05g009170.1	-2,49	6,69E-05	Zinc finger protein 6	Zinc finger protein 6
Solyc02g086700.2	-2,47	2,51E-16	Glucan endo- -beta-glucosidase	Beta-1 3-glucanase Glycoside hydrolase
Solyc07g049530.2	-2,40	6,25E-28	1-aminocyclopropane-1-carboxylate oxidase 1	1-aminocyclopropane-1-carboxylate oxidase
Solyc09g010990.2	-2,35	1,14E-04	Laccase-17	Laccase
Solyc08g081470.2	-2,33	6,95E-06	Protein spiral1	Nitrilase-associated protein
Solyc00g174330.2	-2,32	7,49E-22	Unknown Protein	Pathogenesis related protein PR-1

Solyc02g082920.2	-2,29	1,66E-19	Class II chitinase	Endochitinase
Solyc09g089930.1	-2,27	1,59E-16	Ethylene-responsive transcription factor 1b	Ethylene responsive transcription factor 1a
Solyc02g064690.2	-2,26	3,36E-09	Probable n-acetyltransferase hls1	Acetyltransferase-like protein
Solyc01g087810.2	-2,14	8,52E-18	Subtilisin-like protease	Subtilisin-like protease
Solyc09g005730.2	-2,14	1,89E-06	Math and lrr domain-containing protein pfe0570w	Plant-specific domain TIGR01589 family protein
Solyc01g087820.2	-2,11	3,34E-19	Subtilisin-like protease	Subtilisin-like protease
Solyc03g025670.2	-2,10	5,24E-18	Predicted: uncharacterized protein LOC101252465	PAR-1c protein
Solyc10g044680.1	-2,09	4,37E-04	Transcription factor myb86	Myb-like transcription factor
Solyc10g075150.1	-2,08	2,09E-23	Non-specific lipid-transfer protein 2	Non-specific lipid-transfer protein
Solyc01g087840.2	-2,08	3,83E-09	Subtilisin-like protease	Subtilisin-like protease
Solyc03g119390.2	-2,01	2,08E-04	Transcription factor bee 1	Transcription factor
Solyc04g040180.2	-2,01	3,00E-04	Methyltransferase ddb_g0268948	S-adenosylmethionine-dependent methyltransferase

Some down-regulated genes are involved in the phenylalanine metabolism. Down-regulated genes coding for enzymes located in these defense-related pathways are showed in figure 34.
Phenylalanine metabolism pathway is regulated by aa amine oxidase. (Solyc08g079430.2): the production of hydrogen peroxide deriving from polyamine. The oxidation carried out by the encoded enzyme has been correlated with cell wall maturation and lignification during development as well as with wound-healing and cell wall reinforcement during pathogen invasion (Cona, 2006). Also Aldehyde dehydrogenase family protein (Solyc06g060250.2) is a very important enzyme in this pathways: Aldehyde dehydrogenases (ALDHs) are responsible for oxidation of biogenic aldehyde intermediates as well as for cell detoxification of aldehydes generated during lipid peroxidation (Končitíková, 2015) (Figure 34).

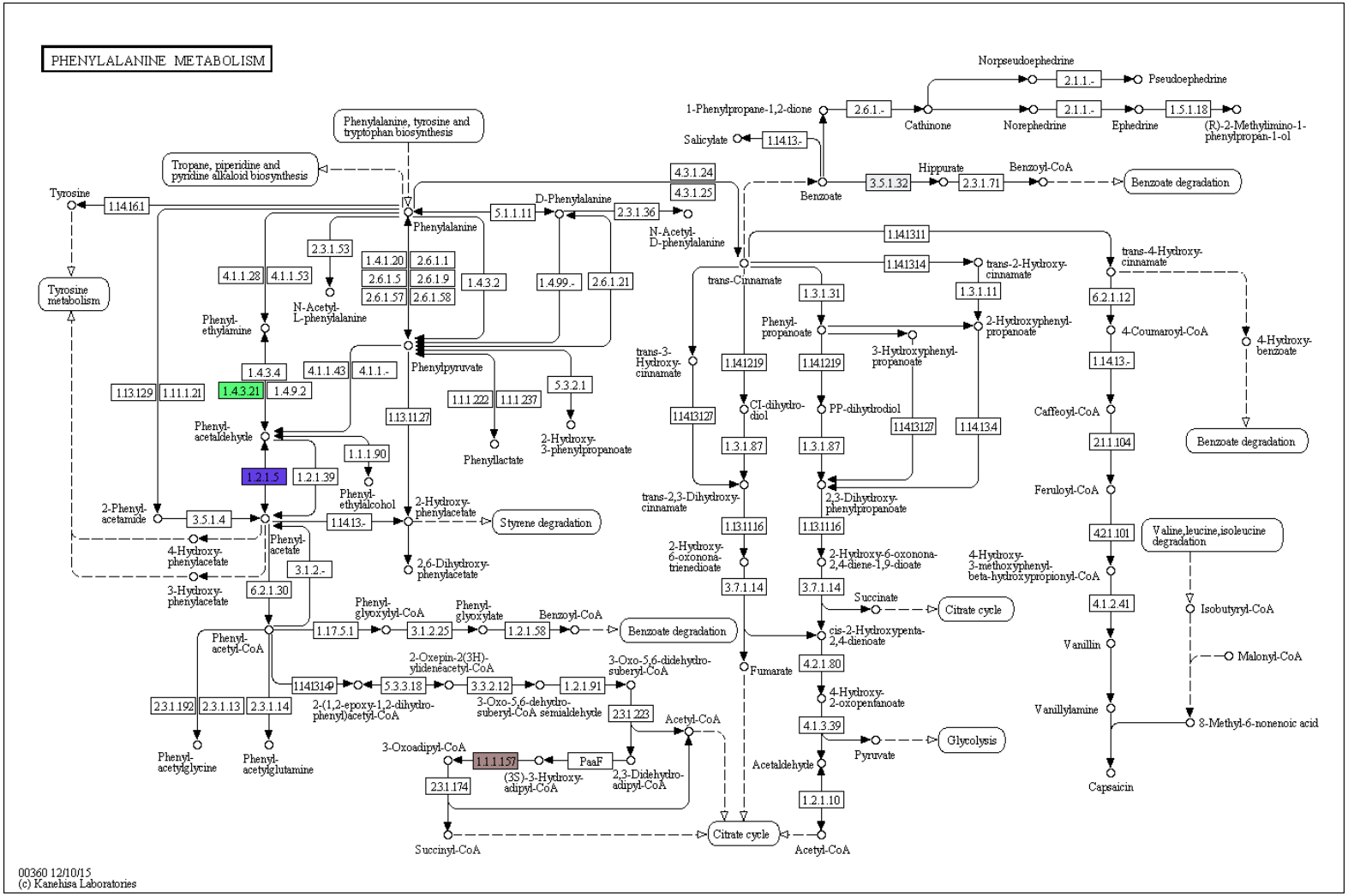


Figure 34: the figure displays the Phenylalanine metabolism. Enzymes whose expression is regulated by the exposition to Sys-treated plants are indicated in green and blue.

4.DISCUSSIONS AND CONCLUSIONS

The environmental stresses are among the major limiting factors on agricultural productivity. A considerable part of world agricultural production is destroyed by parasites causing losses of principal cash crops estimates ranging from 26 to 40% (Oerke, 2006). Crop protection allows safeguarding crop productivity but control strategies based on the use of pesticides are not always compatible with a sustainable agriculture. On the contrary, the use of resistant crops and natural molecules is a major goal of integrated pests management (IPM), an ecosystem-based strategy that focuses on long-term prevention of pests or their damage through a combination of techniques, minimizing risks to people and the environment (https://www.epa.gov/managing-pests-schools/introduction-integrated-pest-management).

In order to limit damages caused by biotic and abiotic stresses, plants have been evolving articulated and interconnected defense mechanisms. These can be constitutive or activated by pests attack; direct or indirect. The direct defenses affects growth and vitality of the pest that feeds or develops on plants. The indirect strategy involves the production of specific compounds, such as extra floral nectar or volatile compounds (VOCs), in response to herbivores infestations. These compounds are able to attract natural enemies of herbivores, such as predators and parasitoids. The improvement of plant endogenous defense strategies is a challenge for the development of more sustainable and safe plant protection system. In this frame, the introduction of transgenic plants enhanced in their defenses, represents a tool, despite the long going debate on GMO.

The evidence for plant-to-plant communication is only a few decades old. A study published in 1983 (Baldwin and Shultz, 1983) demonstrated that poplars and sugar maples can warn each other about insect attacks: intact, undamaged trees near ones infested with herbivores, released herbivore-repelling chemicals to ward off attack. The authors suggested that the injured trees were alerting neighbors of the presence of predators by releasing chemical signals into the air. These results were firstly considered with skepticism by the plant research community, due to methodological problems. However, rigorous and carefully controlled experiments (Karban et al., 2000) overcame those early criticisms. The science of plant communication is now well established and several examples of plant communication, considered the base of defense priming reaction, are available in the scientific literature showing that the communication occurs also between different plant species. Kessler and collaborators (2006) studied VOCs as airborne signals between neighbour sagebrush and tobacco plants. They demonstrated that *Manduca sexta* larvae fed on tobacco exposed to damaged sagebrush had high mortality level.

A deeper understanding of plant signalling pathways lead to the discovery of natural compounds called “elicitors” that induce defense responses. In a pioneer study a beta-glucosidase isolated from *Pieris brassicae* was found to induce terpenoids release from leaves of cabbage (Mattiaci et al., 1995). The first non enzymatic elicitor of plant volatile emission, N-(17-hydroxylinolenoyl)-l-Gln, was identified in beet armyworm (*Spodoptera exigua*) oral secretions (OS) and termed volicitin (Alborn et al., 1997). The authors demonstrated that the VOCs blend following volicitin application on damaged corn leaves was similar to the one released by corn plants attacked by *Spodoptera exigua*.

Plant defense responses are induced not only by molecules from preying organisms but also by endogenous host derived molecules that are released upon injury and/or infection and recognized as danger/alarm signals. Endogenous elicitors include reactive oxygen species (ROS), oligosaccharide and protein fragments (Chai et al., 1987; Albersheim and Anderson, 1971; Pearce et al., 1991). In addition, these molecules are exploited by the plant to amplify defense responses by increasing their production through enzymatic activity. For example, cell wall fragment signals are produced by polygalacturonase while NADPH oxidase generate ROS signals. Both enzymes are induced by mechanical wounding or by biotic stress (Bergey et al., 1999; Torres et al 2002). Correspondingly, the genes encoding the precursors of endogenous peptide elicitors are induced by biotic stress or mechanical wounding (Pearce et al., 2001; Huffaker et al., 2011). The proteolytic enzymes that process peptide's precursors to release the bioactive molecules have not yet been identified, but presumably they too are induced by biotic stresses and wounding. A few plant defense peptides have been identified. According to their functions they may be classified in peptide regulating anti-herbivory responses, Sys, HypSYS, inceptins and ZmPep3, and peptides that induce defense against pathogens, AtPeps, some Zm Peps, GmSubPep and GmPep914 (Yamaguchi and Huffaker, 2011; Huffaker et al., 2013).

Two Hydroxyproline-rich systemins of 18 aa, both deriving from the same precursor protein, were identified in tobacco. Transgenic plants overexpressing HypSys induced defense-related genes encoding JA biosynthetic enzymes, protease inhibitors or pathogenesis related genes (Pearce et al., 2001). In addition, tobacco plants overexpressing preproHypSys were more resistant to herbivory by *Helicoverpa armigera* larvae (Ren and Lu, 2006). Orthologs have been identified in tomato and other solanaceous plants (Pearce and Ryan, 2003; Pearce et al., 2009). Inceptins are 11–13 aa peptides isolated from the oral secretions of *Spodoptera frugiperda* larvae, that induced ethylene production in *Vigna ungiculata* (Schmelz et al., 2006). These peptides are derived from the cowpea chloroplastic ATP synthase following digestion by proteolytic enzymes in the *S. frugiperda* larval gut (Schmelz et al., 2007). Among the maize Pep family, ZmPep3, a 23 aa peptide, has been shown to regulate both direct and indirect anti-herbivory defense in maize and other plant species (Huffaker et al., 2013). AtproPep1 is a 23 aminoacid, derived from the C-terminus of a 92 aa precursor protein, that promote pathogen defense genes, such as PR-1 and PDF1.2 (Huffaker et al., 2006). A similar peptide was also identified in maize (Huffaker et al., 2001). GmSubPep and GmPep914 are two peptides identified in soybean. The former is a 12 aa peptide enclosed in a soybean subtilase. Both peptides induced the expression of defense related genes (Pearce et al., 2010; Yamaguchi et al., 2001).

In the family *Solanaceae,* Systemin is the primary signal able to activate a cascade of reactions in response to wounding and herbivorous insects which leads to the activation of several defense genes (Ryan, 2000). Sys is released from the C-terminal region of a larger precursor of 200 aa without traditional N-terminal secretion signals. The activation of defense genes by systemin is mediated by the octadecanoid signaling pathway (Ryan, 2000). Systemin has been widely characterized in its involvement in the modulation of direct and indirect defenses. The former are characterized by the production of PI and other compounds interfering with larval growth and vitality (McGurl et al., 1992; McGurl et al., 1994; Ryan and Pearce, 1998; Ryan, 2000; Schaller, 2009; Coppola et al., 2014); the latter are

characterized by the production of volatile blends attractive for insect parassitoids (Corrado et al., 2007; Degenhardt et al., 2010).
To evaluate systemin peptide effect in the modulation of tomato anti herbivore defense priming, both tomato plants overexpressing prosystemin and plants with systemin foliar treatment were used. As internal control of the experimental system, tomato plants chewed by *S. littoralis larvae* were used.
The research activity was initially focused on the evaluation of the suitability of the experimental conditions to be sure that plant exposure to source were adequate. The increased expression of defense genes in receiver plants, after exposure in closed boxes, proved that the conditions used were effective for the induction of defense priming in the receiving plants.
The increased expression of defense related genes in tomato plants chewed by phytophagous larvae was verified in a time course experiment. Both early, *ProSys,* lipoxygenase C (*LoxC*) and allene oxide synthase (*AOS*), all involved in JA biosynthesis, and late, *InhI*, genes were analysed. The analysis was carried out in the proximal leaves, where the damage occurred, and in the distal leaves to check the activation of systemic defenses. As expected, the results showed that insect chewing induced the transcription of *ProSys* exclusively at the site of damage, in accordance with its role as an early signal. In addition, ProSys transcription is moderately upgraded, since also few molecules of the signal activate the responses cascade (Ryan, 2000). The over expression of *LoxC* and *AOS*, genes is also expected as the encoded enzymes contribute to the biosynthesis of JA, a powerful activator of late defense gene. *LoxC* belong to the Lipoxygenase gene family, enzymes which catalyze redox reactions of polyunsaturated fatty acids for the formation of unsaturated hydroperoxides (Porta and Rocha-Sosa, 2002). Their main function is to convert the linoleic acid, derived from the activity of phospholipase A2 triggered by the signal of mechanical damage and/or wounding, (Narváez-Vasquez et al., 1999), in a signal molecule such as the (9Z,11E)-(13S)-13-idroperossioctadeca-9,11-dienoate, later converted into precursor of jasmonic acid by the action of the enzyme encoded by *AOS* gene (Froehlich et al., 2001). The expression analysis showed that *LoxC* gene, activated earlier than *AOS* within the pathway, has a variable trend of expression although after 9 hours of chewing a significant up-regulation is observed. *AOS* is activated rapidly and its induction increases during the experimental time. Its up-regulation is observed exclusively at the wound site. These data are in concordance with theories that identify Sys as the starting signal at a damaged site responsible for the JA biosynthesis, a hormone that represent the long-distance mobile signal that mediates the systemic response of the plant (Howe 2005; Sun et al., 2011). The high expression levels observed for *InhI* gene was also expected considering the role of the encoded protein that counteract insect pest attacks. All together the data show that at the chewed site it is observed the induction of *ProSys*, *LoxC* and *AOS* that stimulate the production of JA which is reflected in local and systemic *InhI* gene activation, involved in the direct protection of the plant. The described expression analysis proved that S1 plants were an appropriate internal control of the set up system. Similarly, the effect of Sys foliar applications on the expression of defense genes was monitored to understand if systemin peptide was perceived at cellular level. The expression analyses proved that the perception occurred, as both *ProSys* and *InhI* genes were overexpressed in comparison with the expression present in the untreated leaves. At pM peptide concentration *ProSys* expression had a 5 fold increase in respect to control. Several Sys concentration induced *InhI* transcript. Interestingly, the peptide was able to

induce InhI transcript even at fM concentration. This data well support the hypothesis of the use of peptide as tool in IPM strategies. Since prosystemin overexpression was associated with a modification of the composition of the VOC blend resulted more attractive for the third trophic level (Corrado et al., 2007; Degenhardt et al., 2010), the ability of RSYS plants in plant-to plant communication, was considered an intersting investigation.

External application of systemin peptide to tomato plants was previously described by Pearce and co-workers (1993). In their experiment, two leaf stage tomato plants were excised at the base of the stem, and placed in a solution with the peptide. Under these conditions tomato plants accumulated large amounts of Protease inhibitors. Here it is demonstrated that the peptide effectively activated gene expression of defense genes with external applications on intact leaf. It is possible to infer that the peptide is internalized in the cell following the interaction with a membrane bound receptor.

Another example of plant peptide that when extenally applied on the leaf stimulates production of jasmonic acid, ethylene, and increased expression of genes associated with herbivory defense, including genes involved in VOC biosynthesis is ZmPep3. Picomolar concentration of synthetized peptide applied on injured leaves induce defense related genes and emit a volatile blend similar to chewed plants (Huffaker et al 2013).

Peptides internalization into plant cell may occur through different mechanisms. Studies have been performed on particular peptides referred to as CPPs (Cell-Penetrating Peptides) able to penetrate both animal and plant cells, depending on their sequence and their charge (Milletti et al., 2012; Liu et al., 2013). A variety of models of cellular translocation have been proposed for molecules positively charged, whose adhesion to cell membrane occurs through nonspecific interaction due to opposite electrical charges. Following adhesion, the internalization occurs by permeation of membrane and the peptide is releases in the cytoplasm (Vives et al., 2003). The internalisation may also occur by non-specific endocytosis or receptor-mediated endocytosis (RME), (Schaller et al., 2000; Di Rubbio and Russianova, 2012). The endocytosis appears to be a diffused mechanism to internalize peptides, and may be clathrin or caveolae dependent (Vives et al., 2003; Conner and Schmid, 2003; Järver and Langel, 2006). Recent studies revealed highly conserved mechanisms behind RME in all eukaryotes, including plants, demonstrating a major role of clathrin as well as post-translational modifications of plasma membrane receptors, such as ubiquitination and phosphorylation. Systemin peptide is most likely internalized through an RME events (Yamaguchi and Huffaker, 2011), although the systemin receptor has not yet been identified (Hind et al., 2010).

Gene transcripts that increased in receiver plants include MAP Kinase and WRKY transcription factors. Protein kinases play a central role in signalling during pathogen recognition and the subsequent activation of plant defense mechanisms however only a few data are available on their involvement in mediating plant responses to herbivore. Virus-induced gene silencing of MAPks compromise prosystemin-mediated resistance to *Manduca sexta* herbivory, demonstrating that kinase activities are essential components of the systemin signaling pathway and most likely function upstream of JA biosynthesis (Kandoth et al., 2007). MAPK activity is induced, both locally and systemically, by oral secretions of herbivores and by mechanical wounding in different plant species (Schäfer et al., 2011; Wu et al., 2007). In addition, in grass species, MAPK activity is activated in the leaves 15 min after exposure to green leaf volatiles (Dombrowski et al., 2011). Here we show that MAP Kinase

activity is also induced in receiver plants where they should participate to the actvation of transcription of antiherbivory genes.
WRKY is a recently identified transcription factor family characterized by presence of the highly conserved WRKY domain which interacts with the conserved cognate binding site, the W box, in target genes (Eulgem et al., 2000). The WRKY transcription factors are involved in multiple biological processes in plants, specially in regulating defense against biotic and abiotic stresses (Eulgem and Somssich 2007; Pandey and Somssich, 2009; Rushton et al., 2010). Transcription factors and other related compounds are a group of actors of transcriptional regulating networks, acting as DNA binding proteins, and triggering and/or repressing the transcription of their target genes. In Arabidopsis, a majority of *WRKY* genes are induced by pathogen infection (Dong et al., 2003). Analysis with both knockout and overexpressing gene indicated that pathogen-induced WRKY transcription factors have a partially redundant negative effect on SA mediated defense but exerted a positive role in JA mediated defense. Two *WRKY* genes, *NaWRKY3* and *NaWRKY6*, coordinate responses to herbivory in *Nicotiana attenuata*. The two WRKY transcription factors regulate expression of jasmonic acid biosynthesis genes (*LOX, AOS, AOC* and *OPR*), thereby increasing the levels of JA and its related compounds. This in turn regulates direct and indirect defences against herbivores (Rushton et al., 2010). The up regulation of *WIRKY* genes following exposure to different Source plants shows that WIRKY transcription factors are also involved in the reactions occurring in the Receiving plants following the perception of volatile signals emitted by the three different sources. In addition, the well described antagonism betwen JA ans SA signaling pathways might be exploited by the plants, through *WIRKY* gene, to increase the level of JA whose signaling pathway plays a crucial role in mediating antiherbivore defense responses.
The active defense responses, which require *de novo* protein synthesis, are regulated through a complex and interconnected network of signaling pathways that mainly involve three plant hormones, salicylic acid, jasmonic acid and ethylene, and which results in the activation of defense genes. However, plant hormone cytokinin may also modulate defense signaling and promote plant pathogen and herbivore resistance although through a still unknown mechanism (Naseem et al., 2014). Knotted1 proteins have been proposed to be involved in the regulation of cytokinin biosynthesis. The up-regulation of the gene encoding for Knotted-like homeobox protein in R3 plants likely bring to an increase of CK acting as enhancer of anty herbivory defense. The evaluation of CK content in primed plants should be carried out to confime this hypothesis.
The R3 receiver plants showed a deep transcriptomic reprogramming activated by plant-to-plant comunications. More than 1000 genes were differentially expressed following exposure to Systemin treated plants. Interestingly, 4 up regulated genes are actors of the phenylpropanoid biosynthetic pathway (Figure 31). The functions of phenylpropanoid compounds in plant defence encompass preformed or inducible physical and chemical barriers against colonization. Induction of phenylpropanoid synthesis under stress conditions in general, is the result of increased transcription of genes encoding the enzymes of this pathway (Dixon et al., 2002). The up-regulation of 4 genes operating in final steps of the biosynthesis of lignin components most likely results in a variation of the strength and stiffness of the cell wall aimed at reducing host invasion.
Volatile signals released by injured plants are known to induce gene expression profile modifications in neighbourhood (Turlings and Tumlinson, 1992; Paré and

Tumlinson, 1999; War et al., 2012). Anti herbivore defense priming, was shown to be activated by green-leaf volatiles (GLVs) in maize. GLV-treated maize plants accumulated higher JA concentrations and produced more VOCs in response to the application of caterpillar regurgitant combined with mechanical wounding (Engelberth et al., 2004). It was also shown that undamaged maize plants exposed to VOCs from *S. littoralis* wounded plants up-regulated defense gene expression and showed a prime production of VOCs emissions. Moreover, larvae fed on the primed maize had a reduced growth and were parasitized by the parasitic wasp *Cotesia marginiventris* attracted by the VOCs released by primed plants (Ton et al., 2007). Similarly, here it is shown that tomato plants exposed to plant damaged by *S. littoralis* reduced the weight and vitality of larvae fed with their leaves and were more attractive for the parassitoid *A. ervi*.

Plants of *Vicia faba* and *Phaseolus vulgaris* damaged by the activity of nutrition and oviposition of *Nezara viridula,* released a mixture of volatile compounds that attracted the parasitoid *Trissolcus basalis* (Colazza et al., 2004). The analysis of the extracts obtained from the legumes revealed that the damage done by *N. viridula* increased the release of some terpenoids such as linalool, β-caryophyllene, 4,8,12-trimethyl-1,3,7,11-tridecatetraene and 4,8-dimethyl-1,3,7-nonatriene, which are most likely involved in the attraction of the parasitoid. Plants are also able to emit different VOC blends depending on the attaking herbivore. For example, tobacco, cotton and maize plants infested by *Heliothis virescens* and *Helicoverpa zea* produced different mixtures of volatile compounds. The parasitoid *Cardiochiles nigriceps Viereck* was able to perceive these differences, using them to distinguished the plants infested by *H. virescens*, from those damaged by *H. zea* (De Moraes et al., 1998). A major difference among the VOC blends of the Recever plants analysed in this study, was the emission of β-ocimene which is released by all Receiver plants beeing absent in control. It was very recently demonstrated that transgenic tobacco plants constitutively producing β-ocimene, primed defense responses by both direct and indirect mechanisms in lima bean (Muroi et al., 2011). In line with these results, here it is demonstrated that β-ocimene is also acting in tomato defense priming against herbivores.

In conclusion, this study demonstrated that systemin is effective in priming anti-hervivory defense responses. Both tomato plants overexpressing prosystemin and plants with systemin foliar treatment clearly promoted the defense responses in receiver plants. Several defense related genes resulted over-expressed and the modified expression profiles proved able to activate both direct and indirect defenses. After 24 hr of esposure, receiver plants effectively conteract larvae infestation by reducing their growth and vitality. In addition, at the same time point, receiver plants showed an increased attraction towards the third trophic level determined by an increase of VOCs that, in Sys treated plants resulted in the release of a blend qualitatively similar to that induced by *S. littoralis* herbivory. Direct application of peptide to plants is an effective mechanism to manipulate defense and a good alternative to the costitutive expression of defense genes. This is particularly interesting when the peptide can be directly applied without leaves injury, as occurs for Systemin that, therefore, may represent a new tool for insect pest control.

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STAGE

From November 2015 to December 2015 stage at the Sequentia Biotech, a bioinformatics company, Barcelona, Spain. During this period it was made the elaboration of the data produced by the sequencing of the tomato transcriptome, with particular attention to the analysis of differentially expressed genes.

PUBLICATIONS

Madonna V., Coppola M., Esposito F., Corrado G., Cascone P., Guerrieri E., Pennacchio F., Rao R.Effetto Della Sistemina Nella Modulazione Del Priming Delle Difese Del Pomodoro. *European PhD Network in "Insect Science" 5th Annual Meeting Orosei, 7 – 8 June 2014.*

Madonna V., Coppola M., Corrado G., Cascone P., Guerrieri E., Pennacchio F., Rao R. Effect Of Systemin In The Modulation Of Priming. *IV Annual Meeting of the Plant Genetic and Biotechnology Network: "Sustainable Energy and Food Production in the post genomic era" Padova, June 15-17, 2015.*

European PhD Network in "Insect Science" 5th Annual Meeting Orosei, 7 – 8 June 2014.

Poster Communication Abstract

EFFETTO DELLA SISTEMINA NELLA MODULAZIONE DEL PRIMING DELLE DIFESE DEL POMODORO

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Le piante rispondono all'attacco di agenti di stress biotico attivando diversi meccanismi di difesache possono essere distinti in diretti ed indiretti. Le difese dirette prevedono la produzione di composti tossici come alcaloidi, terpenoidi, polifenoli, inibitori di proteasi e polifenolo ossidasi che interferiscono con l'attività degli enzimi digestivi; i meccanismi di difesa indiretti, invece, includono tutti quei tratti e composti, spesso volatili (VOCs) coinvolti nell'attrazione di nemici naturali come predatori e parassitoidi. Negli ultimi dieci anni, i VOCs sono stati associati alla segnalazione aerea intra- e inter-pianta. Le piante cresciute nelle vicinanze di piante attaccate sviluppano uno stato di "pre-allerta", che le rende più veloci o più efficienti nell'attivazione delle risposte di difesa in seguito ad attacco di erbivori. Tale fenomeno è denominato "Priming".
Nella famiglia delle Solanaceae le sistemine sono una famiglia di peptidi coinvolti nei primi eventi di attivazione di geni di difesa in risposta a ferita e agli attacchi di erbivori masticatori.
L'espressione costitutiva del gene della ProSistemina in piante di pomodoro è risultata associata all'attivazione di geni coinvolti nella produzione di composti organici volatili e nella conseguente modificazione della miscela di volatili rilasciati dalle piante.
Queste osservazioni hanno motivato uno studio più approfondito delle modificazioni indotte dalla Sistemina a ridosso dei VOCs e dei possibili effetti su piante adiacenti. Il possibile impatto sul trascrittoma in piante di pomodoro non attaccate è stato valutato in seguito all'esposizione di tali piante a 3 tipi di sorgenti: piante transgeniche esprimenti in maniera costitutiva il gene della ProSistemina, piante non trasformate su cui sono eseguite applicazioni fogliari del peptide Sistemina sintetico e piante non trasformate masticate da larve di Spodoptera Littoralis. Il monitoraggio del priming è stato eseguito, inizialmente, mediante analisi di espressione in time course di geni candidati medianteReal-Time PCR. L'analisi ha mostrato una regolazione differenziale dell'espressione dei geni in esame nelle 3 condizioni, confermando che piante di pomodoro non attaccate allevate in vicinanza a piante in cui le risposte di difesa siano attivate da diverse condizioni di stress, mostrano uno stato di pre-allerta specifico.

parole chiave: pomodoro, Sistemina, priming, volatili, analisi di espressione

Communication Abstract

EFFECT OF SYSTEMIN IN THE MODULATION OF PRIMING

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Keywords: volatile, expression analysis, sources, receivers.

Plants respond to biotic stress agent attacks by activating various defense mechanisms that can be distinguished in: direct, if they promote toxic compounds release with the aim to interfere with the activity of digestive enzymes or insect life cycle; indirect defense mechanisms, instead, include all traits involved in the attraction of natural enemies such as predators and parasitoids. Over the past decade, plant volatile organic compounds (VOCs) have been linked to signaling intra- and inter-plant. Plants grown near of attacked plants develop a "pre-alert" state, which makes them faster or more efficient in the activation of defense responses to herbivoreattacks. This phenomenon is called "Priming".
In the Solanaceae, systemins are a family of peptides involved in the early events of activation of defense genes in response to injury and to attack by chewing herbivores. The constitutive expression of Prosystemin cDNA in tomato plants was associated to the activation of genes involved in the production of VOCs and the consequent modification of the volatile blend released by transgenic plants and the attractiveness towards natural enemies.
These observations motivated a more detailed study of the changes induced by systemin to the VOCs and the possible effects on near plants.
Primed state in non-attacked tomato plants was evaluated following the exposure to 3 kinds of VOCs sources: transgenic plants expressing Prosystemin cDNA, plants with foliar applications of systemin recombinant peptide and plants chewed by Spodoptera littoralis larvae. Expression analysis of a set of candidate genes in time course was performed by Real-Time RT-PCR underlining that VOCs released by the three different sources were all perceived by receiver plants.
In order to evaluate the biological effects of VOCs emitted by the assayed plants sources, we tested the attractiveness of receivers plants towards the aphid parasitoid Aphidius aervi. This Analysis revealed that the receiver plants exposed to all kind of sources under investigation have a better performance of attractiveness towards the parasotoid compared to the control.
The obtained results indicated that the VOCs released by the different sources were all perceived and active in receiver plants, suggesting that these resulted in a primed state. Moreover, an interesting finding is that external application of recombinant systemin peptide is active in this process, so it represents a useful tool for integrated pest management.

APPENDIX

Table 1: List of UP-regulated genes; the genes description were obtained according to Blast2GO and AgriGO annotations

Locus	logFC	PValue	Blast2GO annotation	AgriGO annotation
Solyc04g077210.2	3,77	1,52E-08	Homeobox protein knotted-1	Knotted-like homeobox protein
Solyc01g094380.2	2,93	9,37E-05	O-glucosyltransferase rumi homolog	Glycosyltransferase CAZy family GT90 (Fragment)
Solyc03g119820.1	2,41	1,06E-03	Oleosin 1	Oleosin Bn-V
Solyc02g078690.1	2,31	6,02E-07	Serine carboxypeptidase	Serine carboxypeptidase K10B2.2
Solyc04g014260.1	2,31	4,46E-05	Zinc-finger homeodomain protein 1	Zinc finger-homeodomain protein 1 (Fragment)
Solyc11g010710.1	2,31	9,10E-05	Ap2-like ethylene-responsive transcription factor ail6	AP2-like ethylene-responsive transcription factor At1g16060
Solyc01g066160.1	2,05	5,38E-04	Unknown Protein	Unknown Protein
Solyc02g089170.2	2,04	3,98E-04	Alpha- -glucan-protein synthase	Alpha-1 4-glucan-protein synthase
Solyc01g007080.2	2,02	1,51E-03	Aluminum-activated malate transporter 8	Aluminum-activated malate transporter (Fragment)
Solyc05g046020.2	1,97	3,32E-08	Peroxidase 3	Peroxidase
Solyc03g020030.2	1,96	1,89E-05	Proteinase inhibitor type-2 cevi57	Proteinase inhibitor II
Solyc04g074900.2	1,96	2,35E-03	40s ribosomal protein s21-	40S ribosomal protein S21
Solyc04g049920.2	1,94	5,51E-04	Rna-binding protein 38-like isoform x2	RNA binding protein-like
Solyc08g082630.2	1,88	4,96E-10	Auxin response factor 9-	Auxin response factor 9
Solyc02g089620.2	1,88	4,36E-09	Proline dehydrogenase mitochondrial	Proline dehydrogenase
Solyc11g013220.1	1,84	3,01E-05	C2h2-like zinc finger protein	Os04g0690100 protein (Fragment)
Solyc02g069280.2	1,78	1,98E-03	Protein argonaute 2	ARGONAUTE 1
Solyc03g005910.2	1,73	4,66E-05	Gdsl esterase lipase at1g29670-	GDSL esterase/lipase At1g29670
Solyc07g041640.2	1,70	1,10E-04	Growth-regulating factor 1-	Growth-regulating factor 1
Solyc04g074340.2	1,68	1,96E-03	7-deoxyloganetin glucosyltransferase-	UDP-glucuronosyltransferase
Solyc01g103500.2	1,67	5,80E-04	Extended synaptotagmin-3	Unknown Protein
Solyc11g042880.1	1,66	3,28E-05	PREDICTED: uncharacterized protein LOC101261986	Harpin-induced protein
Solyc06g053870.2	1,66	1,25E-06	3-ketoacyl- synthase 19-	Fatty acid elongase 3-ketoacyl-CoA synthase
Solyc08g074620.1	1,65	8,78E-16	Polyphenol oxidase	Polyphenol oxidase

Solyc03g115120.1	1,65	1,72E-07	Dnaj homolog subfamily c member 21	Chaperone protein dnaJ
Solyc02g030460.2	1,64	4,53E-04	Methyl- -binding protein 2-like isoform x2	Sh4 homologue protein
Solyc07g055180.2	1,61	8,12E-05	Serine threonine-protein kinase cdl1	Receptor protein kinase-like protein
Solyc10g007800.2	1,60	9,49E-04	Protodermal factor 1-	Meiosis 5
Solyc10g087030.1	1,58	3,15E-04	Premnaspirodiene oxygenase-	cytochrome P450
Solyc04g078460.2	1,58	7,24E-04	Probable isoaspartyl peptidase l-asparaginase 2	N(4)-(Beta-N-acetylglucosaminyl)-L-asparaginase
Solyc00g138060.2	1,56	9,87E-04	Unknown Protein	2-oxoglutarate-dependent dioxygenase
Solyc08g083240.2	1,56	5,76E-08	Protein iq-domain 1-	Calmodulin-binding protein family-like
Solyc04g050570.2	1,56	9,79E-08	Gdsl esterase lipase at5g33370-	GDSL esterase/lipase At5g33370
Solyc10g048190.1	1,55	1,46E-04	Thymocyte nuclear protein 1	Ubiquinol-Cytochrome c reductase iron-sulfur subunit
Solyc01g007200.2	1,53	3,92E-04	PREDICTED: uncharacterized protein LOC101262337 isoform X1	Unknown Protein
Solyc11g011310.1	1,53	8,24E-05	Probable rhamnogalacturonate lyase b	Rhamnogalacturonate lyase
Solyc10g074440.1	1,51	7,74E-10	Chit_soltu ame: full=endochitinase flags: precursor	Endochitinase (Chitinase)
Solyc03g122360.2	1,51	1,29E-04	Cytochrome p450 71a1	Cytochrome P450
Solyc01g089910.2	1,50	2,65E-03	Flotillin-like protein 6	Flotillin domain protein
Solyc07g055750.2	1,49	1,15E-03	Strictosidine synthase 1	Strictosidine synthase-like protein
Solyc02g033040.2	1,48	3,78E-04	F-box kelch-repeat protein at3g23880-	F-box family protein
Solyc02g078850.1	1,47	9,28E-08	Shematrin-like protein 2	Unknown Protein
Solyc01g098620.2	1,46	8,76E-04	Predicted: uncharacterized protein LOC102588527	Unknown Protein
Solyc08g066220.2	1,46	3,04E-04	Histidine decarboxylase-	Decarboxylase family protein
Solyc04g009040.2	1,45	1,97E-04	Probable lrr receptor-like serine threonine-protein kinase at3g47570	Receptor like kinase%2C RLK
Solyc09g098010.2	1,44	2,26E-03	Geraniol 8-hydroxylase-	Cytochrome P450
Solyc04g081080.1	1,44	2,13E-04	Probable lrr receptor-like serine threonine-protein kinase at4g36180	Receptor like kinase%2C RLK
Solyc09g072750.2	1,43	7,32E-08	Repetitive proline-rich cell wall protein 2-	Unknown Protein
Solyc06g071640.2	1,42	6,09E-04	Tryptophan aminotransferase-related protein 2-	Alliinase (Fragment)
Solyc03g007690.1	1,41	7,95E-06	Abc transporter g family member 8-	ABC transporter G family member 8
Solyc09g082790.2	1,41	1,06E-05	Meiotic recombination protein dmc1 homolog	DNA repair and recombination protein RAD51
Solyc07g052980.2	1,41	4,34E-05	Xyloglucan endotransglucosylase hydrolase protein 9	Xyloglucan endotransglucosylase/hydrolase 5
Solyc04g077170.2	1,40	2,76E-05	Epidermal patterning factor-like protein 2	EPIDERMAL PATTERNING FACTOR-like protein 2
Solyc01g066640.2	1,38	6,92E-06	Uncharacterized serine-rich	Os04g0405500 protein (Fragment)
Solyc06g061230.2	1,38	5,92E-05	Metallocarboxypeptidase inhibitor	Unknown Protein
Solyc06g072310.2	1,38	2,08E-06	Homeobox-leucine zipper protein hdg11-	Homeobox-leucine zipper protein PROTODERMAL FACTOR 2
Solyc01g079980.2	1,38	2,85E-04	Basic 7s globulin-	Xylanase inhibitor (Fragment)

Solyc07g056460.2	1,37	4,28E-04	Probable glutathione s-transferase	Glutathione S-transferase-like protein
Solyc03g033350.2	1,36	2,32E-03	Aspartic proteinase- protein 1	Aspartyl protease family protein
Solyc01g057320.1	1,35	5,92E-05	Phragmoplast orienting kinesin-1 isoform x1	Kinesin-like protein
Solyc01g111350.2	1,35	2,50E-04	Probable transporter mch1	Nodulin family protein
Solyc09g064230.1	1,34	2,16E-03	Multiple c2 and transmembrane domain-containing protein 1	Phosphoribosylanthranilate transferase (Fragment)
Solyc04g077140.2	1,34	4,08E-08	Formin-like protein 18	Unknown Protein
Solyc07g007860.1	1,32	2,68E-06	Kda proline-rich	Proline rich protein (Fragment)
Solyc09g006010.2	1,32	1,94E-08	Pathogenesis-related leaf protein 4	Pathogenesis related protein PR-1
Solyc01g091010.2	1,31	3,90E-04	Axial regulator yabby 1	YABBY-like transcription factor CRABS CLAW-like protein
Solyc00g156980.2	1,30	7,41E-08	Unknown Protein	Choline dehydrogenase
Solyc09g005630.2	1,30	1,36E-04	Protein trichome birefringence	Os03g0291800 protein (Fragment)
Solyc01g095750.2	1,30	2,13E-03	Long chain acyl- synthetase 4	Long-chain-fatty-acid-CoA ligase
Solyc03g113970.2	1,30	2,29E-03	Calmodulin binding isoform 2	Calmodulin binding protein
Solyc05g051290.2	1,29	1,74E-06	Hmg-y-related protein a-	High mobility group family
Solyc10g007830.1	1,29	6,72E-04	Protein too many mouths-	LRR receptor-like serine/threonine-protein kinase%2C RLP
Solyc12g019480.1	1,29	1,14E-04	Formin-like protein 2	Formin 3
Solyc01g008600.2	1,29	1,63E-06	Zinc finger ccch domain-containing protein 53-	Zinc finger CCCH domain-containing protein 53
Solyc04g074310.2	1,29	4,12E-06	Rna-binding protein 38-	RNA-binding protein 68390-68829
Solyc02g080330.2	1,28	7,14E-07	Cytochrome p450 77a1	Cytochrome P450
Solyc07g049430.2	1,28	1,51E-05	Gdsl esterase lipase at2g04570	GDSL esterase/lipase At2g42990
Solyc07g054950.1	1,28	5,52E-06	Cyclin-d6-1	Cyclin D2
Solyc08g008020.1	1,28	5,92E-05	Multiple c2 and transmembrane domain-containing protein 1	Phosphoribosylanthranilate transferase (Fragment)
Solyc10g084290.1	1,27	1,86E-05	Interactor of constitutive active rops chloroplastic-like isoform x1	Interactor of constitutive active ROPs 3
Solyc12g056190.1	1,27	1,45E-03	Nuclear transport factor 2 family protein	Nuclear transport factor 2 (NTF2)-like protein
Solyc01g111740.2	1,26	1,98E-04	PREDICTED: uncharacterized protein LOC101255743	Bzip-like transcription factor-like
Solyc09g062970.1	1,26	4,43E-06	Unknown Protein	Unknown Protein
Solyc03g006800.1	1,26	2,73E-04	Transcription factor tcp9-	TCP family transcription factor
Solyc01g066910.2	1,26	5,74E-08	Lipid-transfer protein dir1	PVR3-like protein
Solyc10g008440.2	1,25	3,86E-04	Expansin beta isoform 1	Expansin B1
Solyc03g113910.2	1,25	1,14E-03	Gibberellin-regulated protein 12-	Gibberellin-regulated protein 2
Solyc11g069960.1	1,24	8,91E-10	Probable leucine-rich repeat receptor-like protein kinase at1g68400	Receptor like kinase%2C RLK
Solyc03g116740.2	1,24	9,90E-06	Phosphatidylcholine:diacylglycerol cholinephosphotransferase 1-	Genomic DNA chromosome 3 P1 clone MSJ11
Solyc09g092720.2	1,24	6,09E-04	Glycine-rich protein 3 short isoform-	Unknown Protein
Solyc10g080430.1	1,23	2,42E-03	Multiple c2 and transmembrane domain-containing protein 1-	Phosphoribosylanthranilate transferase (Fragment)

Solyc01g111950.2	1,23	5,09E-04	Receptor-like cytosolic serine threonine-protein kinase rbk1 isoform x1	Receptor-like kinase
Solyc02g087510.2	1,22	1,79E-03	Serine threonine-protein kinase d6pkl2	Ribosomal protein S6 kinase alpha-2 protein kinase
Solyc03g121600.2	1,22	8,97E-06	Protein hothead-like isoform x2	Choline dehydrogenase
Solyc04g005600.1	1,22	4,81E-05	Protein odorant1-	MYB transcription factor
Solyc09g098490.2	1,21	4,50E-05	Clathrin interactor epsin 2 isoform x2	Epsin 2
Solyc02g085490.1	1,21	5,79E-05	Spindle assembly abnormal protein 6	Os12g0581300 protein (Fragment)
Solyc08g080590.2	1,21	6,78E-06	Osmotin-like protein	Osmotin 81 (Fragment)
Solyc06g060860.1	1,21	1,73E-03	Atp-dependent caseinolytic protease crotonase family protein	Unknown Protein
Solyc06g065340.1	1,20	2,31E-05	PREDICTED: uncharacterized protein LOC101251995	Unknown Protein
Solyc06g072290.2	1,20	1,56E-04	Golgin candidate 5-	Protein Kinase interacting protein
Solyc07g056360.1	1,20	1,42E-03	Transcription factor par1	Unknown Protein
Solyc02g080610.2	1,20	3,85E-05	Ankyrin repeat domain-containing protein 13c	Ankyrin repeat domain-containing protein 13C-A
Solyc02g090960.1	1,20	2,75E-06	Protein ralf-	Rapid alkalinization factor 3
Solyc10g080870.2	1,20	1,00E-05	Cytochrome p450 86b1-	Cytochrome P450
Solyc12g043030.1	1,20	5,21E-04	Probable sulfate transporter	Sulfate transporter
Solyc04g063390.2	1,19	1,06E-05	Chaperone protein dnaj 10	Chaperone protein dnaJ 10
Solyc06g007890.2	1,19	1,38E-04	Gibberellin-regulated protein 5-	Gibberellin regulated protein
Solyc01g097110.1	1,19	9,49E-05	Fanconi anemia group d2 protein homolog	Fanconi anemia group D2 protein
Solyc01g107730.2	1,18	2,84E-04	D-type cyclin family 3 subgroup 2	Cyclin
Solyc09g010960.2	1,18	2,02E-03	Probable wrky transcription factor 49	WRKY transcription factor 17
Solyc02g078400.2	1,17	4,83E-07	Allantoinase	Allantoinase
Solyc08g075240.2	1,17	4,75E-05	Long-chain-alcohol oxidase fao4a-	Glucose-methanol-choline oxidoreductase
Solyc06g065970.1	1,16	1,83E-04	14 kda proline-rich	Cortical cell-delineating protein
Solyc03g115870.2	1,16	1,23E-03	Thioredoxin- chloroplastic	Thioredoxin 2
Solyc01g091230.2	1,16	5,17E-05	Lrr receptor-like serine threonine-protein kinase gso1	Receptor like kinase%2C RLK
Solyc08g081790.1	1,16	2,71E-03	Disease resistance response protein 206-	Dirigent protein
Solyc06g007170.2	1,15	1,37E-04	Protein pmr5-	Os06g0207500 protein (Fragment)
Solyc11g011000.1	1,15	4,92E-04	Cysteine-rich repeat secretory protein 60-	Cysteine-rich repeat secretory protein 60
Solyc03g118370.2	1,15	6,21E-08	Serine carboxypeptidase-	Serine carboxypeptidase K10B2.2
Solyc07g064990.2	1,15	6,48E-05	Indole-3-acetate o-methyltransferase 1-	S-adenosyl-L-methionine salicylic acid carboxyl methyltransferase-like protein
Solyc04g013200.1	1,15	2,45E-04	PREDICTED: uncharacterized protein LOC101247604	Unknown Protein
Solyc08g078940.1	1,15	4,85E-07	14 kda proline-rich	Cortical cell-delineating protein
Solyc01g068140.2	1,15	1,19E-04	3 -n-debenzoyl-2 -deoxytaxol n-benzoyltransferase	10-deacetylbaccatin III-10-O-acetyl transferase-like

Solyc07g018290.2	1,14	4,19E-05	Ap2-like ethylene-responsive transcription factor ail5 isoform x2	AP2-like ethylene-responsive transcription factor At1g16060
Solyc01g088400.2	1,14	1,18E-03	Protein eceriferum 1-	CER1
Solyc10g055730.1	1,14	1,00E-03	Uncharacterized acetyltransferase at3g50280-	N-hydroxycinnamoyl/benzoyltransferase 4
Solyc06g008770.1	1,14	2,45E-03	Nbs-lrr resistance protein	Cc-nbs-lrr%2C resistance protein
Solyc03g118770.2	1,13	1,23E-03	Wuschel-related homeobox 1	WUSCHEL-related homeobox-containing protein 4
Solyc02g071870.2	1,13	8,14E-04	Probable lrr receptor-like serine threonine-protein kinase rfk1 isoform x1	Receptor like kinase%2C RLK
Solyc06g084080.2	1,13	6,01E-04	Guanylate-binding protein 4 isoform x1	Guanylate-binding family protein
Solyc11g005710.1	1,13	1,38E-04	Wd repeat-containing protein 44	WD-40 repeat family protein
Solyc05g053550.2	1,13	1,22E-05	Chalcone synthase	Chalcone synthase
Solyc10g005400.2	1,12	8,97E-04	Inositol oxygenase 1-	Inositol oxygenase
Solyc02g072490.2	1,12	1,85E-03	O-fucosyltransferase family protein isoform 1	Os01g0841200 protein (Fragment)
Solyc09g061930.2	1,12	4,05E-05	Kinase-like protein tmkl1	Receptor like kinase%2C RLK
Solyc06g005980.2	1,11	1,67E-03	Anthranilate synthase alpha subunit chloroplastic-like isoform x1	Anthranilate synthase component I-1
Solyc03g115200.2	1,11	5,93E-04	Plasmodesmata callose-binding protein 3-	Glucan endo-1 3-beta-glucosidase 1
Solyc03g117560.2	1,11	8,39E-05	Lamin-like protein	Blue copper-like protein
Solyc06g060360.2	1,11	2,28E-04	Adenine nucleotide alpha hydrolases-like superfamily protein	Universal stress protein family protein
Solyc11g008830.1	1,11	6,15E-04	Lob domain-containing protein 6-	LOB domain protein
Solyc06g073560.2	1,11	1,04E-03	Isovaleryl- mitochondrial	Isovaleryl-CoA dehydrogenase
Solyc02g079370.2	1,10	1,15E-04	Cyclin-d6-1 isoform x1	Cyclin-D6-1
Solyc12g015690.1	1,10	7,66E-05	Fasciclin-like arabinogalactan protein 1	Fasciclin-like arabinogalactan protein 10
Solyc01g099650.2	1,09	2,10E-04	Formin-like protein 11	Formin 3
Solyc04g077490.2	1,09	3,79E-05	Ap2-like ethylene-responsive transcription factor ant	AP2-like ethylene-responsive transcription factor At1g16060
Solyc11g011300.1	1,09	1,94E-03	Probable rhamnogalacturonate lyase b	Rhamnogalacturonate lyase
Solyc07g049370.2	1,09	3,85E-04	Glucan endo- -beta-glucosidase 12	Glucan endo-1 3-beta-glucosidase A6
Solyc01g006320.2	1,09	1,49E-04	Protein ndr1-	Non-race specific disease resistance protein 1-like protein b
Solyc07g018070.2	1,09	1,78E-05	Double clp-n motif-containing p-loop nucleoside triphosphate hydrolases superfamily	Heat shock protein-related (Fragment)
Solyc02g094190.2	1,09	7,95E-04	Probable transporter mch1	Nodulin family protein
Solyc07g055950.2	1,08	4,18E-04	Protodermal factor 1-	Meiosis 5
Solyc07g008010.2	1,08	7,71E-04	Transcription factor myb82-	Myb transcription factor
Solyc06g076220.2	1,08	1,47E-05	Expansin-a6-	Expansin-1
Solyc03g123590.2	1,08	9,40E-04	Dna binding	Remorin family protein
Solyc06g068550.2	1,08	3,38E-05	Protein aspartic protease in guard cell 2-	Aspartic proteinase nepenthesin-1
Solyc04g080490.2	1,08	4,79E-06	Zinc-finger homeodomain protein 5-	Zinc finger-homeodomain protein 1 (Fragment)

Solyc04g078770.2	1,07	7,96E-04	Heat stress transcription factor b-4	Heat stress transcription factor
Solyc01g107370.2	1,07	2,61E-04	Gibberellin-regulated protein	Gibberellin-regulated family protein
Solyc03g026040.2	1,07	3,45E-04	Leucine-rich repeat receptor protein kinase exs	Receptor like kinase%2C RLK
Solyc10g045290.1	1,07	7,42E-04	Intracellular protein transport protein uso1-	Kinase interacting family protein
Solyc06g068880.2	1,07	8,76E-06	Unknown Protein	Serine carboxypeptidase 1
Solyc03g119990.2	1,07	3,81E-04	PREDICTED: uncharacterized protein LOC101253985	Hydrolase alpha/beta fold family protein
Solyc09g061280.2	1,06	2,40E-03	Cyclin-dependent kinase inhibitor 3-	Cyclin dependent kinase inhibitor
Solyc03g121170.2	1,06	1,08E-04	Gdsl esterase lipase apg-	GDSL esterase/lipase At5g22810
Solyc03g006840.2	1,06	3,99E-05	Protein longifolia 1-	Genomic DNA chromosome 5 P1 clone MTG10
Solyc01g088380.1	1,06	3,62E-05	Dna replication atp-dependent helicase nuclease dna2 isoform x1	DNA helicase
Solyc09g065240.2	1,06	1,28E-03	Probable inactive patatin-like protein 9	Patatin-like protein 3
Solyc01g100750.2	1,06	8,90E-04	PREDICTED: uncharacterized protein LOC101254641	Susceptibility homeodomain transcription factor (Fragment)
Solyc02g090480.2	1,06	7,23E-04	Peptidyl-prolyl cis-trans isomerase cyp40-	Peptidyl-prolyl cis-trans isomerase D
Solyc08g063090.2	1,06	6,70E-04	Delta -fatty-acid desaturase 2-	Delta-6-desaturase
Solyc02g089130.2	1,05	1,96E-04	Cobra-like protein 4	COBRA-like protein
Solyc08g075680.2	1,05	5,44E-04	Coiled-coil domain-containing protein 136 isoform x1	Unknown Protein
Solyc08g005630.2	1,05	3,50E-06	Long-chain-alcohol oxidase fao4a-	Glucose-methanol-choline oxidoreductase
Solyc01g096070.2	1,04	2,55E-05	Auxin response factor 18	Auxin response factor 9
Solyc01g007800.2	1,04	4,90E-05	Transcription repressor ofp6-	Plant-specific domain TIGR01568 family protein
Solyc01g096450.2	1,04	1,71E-03	Protein aspartic protease in guard cell 2-	Aspartic proteinase nepenthesin-1
Solyc09g030450.2	1,04	1,91E-04	Probable inactive receptor kinase at5g58300	Receptor like kinase%2C RLK
Solyc10g084380.1	1,04	1,19E-05	Wrky transcription factor 44	WRKY transcription factor 42 (Fragment)
Solyc10g018780.1	1,04	2,45E-03	Squamosa promoter-binding-like protein 8	Squamosa promoter binding protein 1
Solyc01g091540.1	1,03	7,00E-04	Growth-regulating factor 9 isoform x1	Growth-regulating factor 12
Solyc05g005320.1	1,03	2,19E-04	PREDICTED: uncharacterized protein LOC101249820	Unknown Protein
Solyc03g031420.1	1,03	1,12E-03	Molybdenum cofactor sulfurase-	Molybdenum cofactor sulfurase
Solyc05g026480.1	1,03	2,20E-03	Transcriptional corepressor leunig-like isoform x2	WD-40 repeat family protein
Solyc10g078680.1	1,03	4,03E-04	Multiple c2 and transmembrane domain-containing protein 1-like	Phosphoribosylanthranilate transferase (Fragment)
Solyc03g005960.2	1,03	3,51E-04	Probable lrr receptor-like serine threonine-protein kinase at1g53420 isoform x1	Receptor like kinase%2C RLK
Solyc08g077990.2	1,02	1,88E-05	Probable serine threonine-protein kinase cdc7	Kinase like protein
Solyc11g072840.1	1,02	1,17E-04	Histone h4	Histone H4
Solyc04g026110.2	1,02	6,06E-06	R2 late blight resistance protein	Cc-nbs%2C resistance protein fragment
Solyc12g007160.1	1,02	1,81E-03	Probable protein abil5	Protein ABIL1

Solyc02g080260.2	1,02	1,36E-06	Homeobox-leucine zipper protein meristem l1-like	Homeobox leucine-zipper protein
Solyc02g080390.2	1,02	1,92E-04	Abnormal spindle- microcephaly-associated protein homolog isoform x1	Abnormal spindle-like microcephaly-associated protein (Fragment)
Solyc02g094520.2	1,02	2,15E-04	Histone-lysine n- h3 lysine-9 specific suvh4	Histone-lysine N-methyltransferase
Solyc09g007330.2	1,02	2,09E-04	Probable dna helicase mcm8 isoform x1	DNA replication licensing factor MCM6
Solyc06g007610.2	1,02	2,04E-05	Lactoylglutathione lyase glyoxalase i family protein	Early tobacco anther 1
Solyc04g080270.2	1,02	8,82E-04	Dentin sialophospho	Genomic DNA chromosome 5 P1 clone MJB21
Solyc09g090680.2	1,02	2,60E-03	Cysteine-rich repeat secretory protein 3-	Cysteine-rich repeat secretory protein 3
Solyc08g068670.2	1,02	1,98E-04	Histidine decarboxylase-	Decarboxylase family protein
Solyc11g068890.1	1,01	4,81E-04	Protein yls9-	NHL1 (Fragment)
Solyc12g005020.1	1,01	1,72E-04	Nep1-interacting 1	Ring H2 finger protein
Solyc11g006250.1	1,01	1,25E-03	Gdsl esterase lipase at5g33370-	GDSL esterase/lipase At5g33370
Solyc07g054170.2	1,01	1,38E-03	Expansin-b3-	Expansin B1
Solyc05g009100.2	1,01	4,23E-05	Probable leucine-rich repeat receptor-like protein kinase at1g68400	Receptor like kinase%2C RLK
Solyc05g015840.2	1,00	4,68E-05	Squamosa promoter-binding-like protein 16	Squamosa promoter-binding protein
Solyc04g077510.2	1,00	5,25E-04	Growth-regulating factor 1-	Growth regulating factor 1 (Fragment)
Solyc03g083510.2	1,00	6,66E-05	Probable lrr receptor-like serine threonine-protein kinase at1g34110	LRR receptor-like serine/threonine-protein kinase%2C RLP
Solyc10g008320.1	1,00	4,39E-05	PREDICTED: uncharacterized protein LOC104649465	Unknown Protein
Solyc02g092420.2	1,00	1,01E-03	Btb poz domain-containing protein at3g49900	Os07g0587200 protein (Fragment)
Solyc06g072660.2	1,00	1,10E-03	Protein dek-like isoform x2	Dek protein
Solyc04g078470.2	0,99	2,21E-04	Cyclin-d3-3-like isoform x2	Cyclin D3-1
Solyc02g072140.1	0,99	6,06E-05	Une1-like protein	UNE1-like protein
Solyc04g076400.2	0,99	1,30E-03	Vin3-like protein 2	Vernalization insensitive 3 (Fragment)
Solyc09g018020.2	0,99	2,54E-03	Expansin alpha	Expansin
Solyc02g070540.2	0,99	8,11E-05	PREDICTED: uncharacterized protein LOC101246207	Os01g0611000 protein (Fragment)
Solyc06g059930.2	0,99	1,97E-04	Germacrene c synthase-	Sesquiterpene synthase 1
Solyc08g082990.2	0,99	1,13E-06	Oligopeptide transporter 7-	Oligopeptide transporter 9
Solyc09g011000.2	0,98	6,54E-04	Laccase-17-	Laccase
Solyc06g072240.1	0,98	1,53E-03	Histone h4	Histone H4
Solyc04g008600.2	0,98	6,45E-04	Timeless-interacting protein	Chromosome segregation in meiosis protein 3
Solyc09g061890.2	0,97	7,07E-04	Probable pectate lyase 8	Pectate lyase 1-27
Solyc07g048100.1	0,97	1,72E-03	PREDICTED: uncharacterized protein LOC101260553 isoform X1	BRCA1 C Terminus domain containing protein expressed
Solyc03g122140.2	0,97	9,62E-04	Peroxisomal -2-hydroxy-acid oxidase glo4-	L-lactate dehydrogenase
Solyc07g066350.1	0,97	1,86E-03	Uncharacterized serine-rich protein	Unknown Protein

Solyc09g042710.2	0,97	2,49E-03	Web family protein at2g38370	Myosin heavy chain-like
Solyc06g051320.2	0,97	1,68E-04	Vinorine synthase-	Transferase family protein
Solyc02g085390.2	0,97	3,54E-04	Atp-dependent dna helicase ddm1 isoform x1	Uncharacterized ATP-dependent helicase C25A8.01c
Solyc04g015620.2	0,96	1,86E-04	PREDICTED: uncharacterized protein LOC101245049	Os01g0611000 protein (Fragment)
Solyc00g099580.1	0,96	2,81E-03	Unknown Protein	Gamma-glutamyltranspeptidase
Solyc09g011820.2	0,96	2,83E-03	Gpi-anchored protein	Unknown Protein
Solyc02g087980.2	0,96	7,31E-04	Structural maintenance of chromosomes protein 4	Structural maintenance of chromosomes protein 4
Solyc01g111840.2	0,96	5,70E-04	Hippocampus abundant transcript-like protein 1 isoform x2	MFS-type drug efflux transporter P55
Solyc03g120930.1	0,96	1,50E-03	Af211533_1avr9 cf-9 rapidly elicited protein 146	Avr9/Cf-9 rapidly elicited protein 146
Solyc01g102310.2	0,96	9,61E-06	Grip and coiled-coil domain-containing	Unknown Protein
Solyc12g044630.1	0,96	7,11E-04	Profilin	Profilin
Solyc08g080280.2	0,95	8,26E-04	PREDICTED: uncharacterized protein LOC101266546	Unknown Protein
Solyc06g076920.2	0,95	2,82E-03	Dehydrodolichyl diphosphate synthase 2-	Undecaprenyl pyrophosphate synthase
Solyc02g089550.2	0,95	2,35E-05	Protein nsp-interacting kinase 1	Receptor like kinase%2C RLK
Solyc12g011010.1	0,95	1,30E-03	Protodermal factor 1-	Meiosis 5
Solyc02g083610.2	0,95	1,06E-03	PREDICTED: uncharacterized protein LOC101264882	BZIP transcription factor
Solyc08g080730.2	0,94	2,53E-03	Tetraspanin-10 isoform x1	Senescence-associated protein
Solyc03g117550.1	0,94	2,73E-04	Receptor-like protein kinase at1g80870	Receptor protein kinase-like
Solyc08g042100.2	0,94	4,63E-05	Arm repeat superfamily protein isoform 1	Armadillo/beta-catenin repeat family protein
Solyc04g075000.1	0,93	1,35E-03	Serine threonine-protein kinase-like protein at3g51990	Serine/threonine protein kinase
Solyc03g083720.1	0,93	2,55E-03	21 kda	Pectinesterase
Solyc02g062780.2	0,92	2,01E-05	Atp-dependent dna helicase ddm1-like isoform x1	Chromodomain-helicase-DNA-binding protein 6
Solyc11g010850.1	0,92	3,97E-05	Probable 1-deoxy-d-xylulose-5-phosphate synthase chloroplastic	1-deoxy-D-xylulose 5-phosphate synthase 2
Solyc07g052240.2	0,92	2,25E-03	L-ascorbate oxidase homolog	Laccase-22
Solyc08g014190.2	0,92	1,80E-03	Geraniol 8-hydroxylase-	Cytochrome P450
Solyc03g093250.1	0,92	1,01E-03	Structural maintenance of chromosomes protein 2-1-	Structural maintenance of chromosomes 2
Solyc03g118740.2	0,92	1,17E-05	Probable auxin efflux carrier component 1c	Auxin efflux carrier
Solyc09g065590.2	0,92	2,53E-03	Auxin canalization protein	Os12g0604200 protein (Fragment)
Solyc08g083210.2	0,91	3,57E-04	Endo- -beta-glucanase	Endoglucanase 1
Solyc07g061920.2	0,91	2,98E-04	Callose synthase 8	Glucan synthase like 3
Solyc12g094700.1	0,91	6,46E-05	Xylem cysteine proteinase 1-	Cathepsin B-like cysteine proteinase
Solyc01g067510.2	0,91	1,05E-03	Proline-rich receptor-like protein kinase perk3 isoform x1	Receptor-like kinase
Solyc01g100030.2	0,91	9,25E-04	Deoxyuridine 5 -triphosphate nucleotidohydrolase	Deoxyuridine 5%26apos-triphosphate nucleotidohydrolase
Solyc06g083490.2	0,90	7,27E-04	Tropinone reductase homolog	Tropinone reductase-like protein 16

Solyc01g080070.2	0,90	3,76E-05	Neurogenic protein mastermind	Copper chaperone
Solyc03g114690.2	0,90	2,87E-04	Wd repeat and hmg-box dna-binding protein 1	Wd-40 repeat-containing protein
Solyc09g009900.2	0,90	9,95E-04	Replication protein a 14 kda subunit b	Pollen-specific protein - like
Solyc09g082830.2	0,90	2,26E-05	Protein argonaute 10	ARGONAUTE 1
Solyc09g090500.2	0,90	3,06E-04	Pavine n-methyltransferase-	Cyclopropane-fatty-acyl-phospholipid synthase
Solyc07g008710.2	0,90	1,52E-03	Mlp-like protein 34-	Major latex-like protein
Solyc09g072820.2	0,90	4,95E-06	Cellulose synthase a catalytic subunit 4	Cellulose synthase
Solyc01g111330.2	0,90	7,72E-04	Thaumatin-like protein 1b	Thaumatin-like protein
Solyc12g015800.1	0,90	1,37E-03	E3 ubiquitin-protein ligase at4g11680	RING finger family protein
Solyc01g080770.2	0,90	7,26E-04	Leucine-rich repeat receptor- serine threonine-protein kinase bam3	Receptor like kinase%2C RLK
Solyc06g069790.2	0,90	1,37E-04	Gibberellin-regulated protein 6-	Gibberellin-regulated protein
Solyc02g093400.1	0,90	2,64E-03	Lipid ii flippase	Integral membrane protein MviN
Solyc07g041970.2	0,90	4,74E-05	Subtilisin-like protease	Subtilisin-like protease
Solyc08g076370.2	0,89	4,41E-06	Homeobox-leucine zipper protein hdg5 isoform x1	Homeobox-leucine zipper protein ATHB-9
Solyc08g077210.2	0,89	3,34E-04	Type i inositol -trisphosphate 5-phosphatase 2-like	Inositol 1 4 5-trisphosphate 5-phosphatase
Solyc10g084150.1	0,89	8,31E-05	Cytokinin riboside 5 -monophosphate phosphoribohydrolase log3	Cytokinin riboside 5%26apos%3B-monophosphate phosphoribohydrolase LOG
Solyc10g080690.1	0,89	9,85E-04	Patatin-like protein 3	Patatin-like protein 3
Solyc01g101030.2	0,88	1,92E-04	Fact complex subunit spt16-	FACT complex subunit SPT16
Solyc07g005840.2	0,88	8,64E-06	Cellulose synthase a catalytic subunit 7	Cellulose synthase 3
Solyc05g056470.1	0,88	7,42E-06	Abc transporter g family member 5	ABC transporter G family member 5
Solyc07g054900.2	0,88	2,57E-03	Polyneuridine-aldehyde esterase-	Alpha-hydroxynitrile lyase
Solyc09g092760.2	0,88	1,24E-03	Glycine-rich cell wall structural isoform x1	Glycine-rich protein
Solyc08g066810.2	0,88	6,20E-04	Cellulase protein	Glycosyl hydrolase family 5 protein/cellulase
Solyc12g100180.1	0,88	6,05E-04	Pleiotropic drug resistance protein 1-	ATP-binding cassette transporter
Solyc09g014160.1	0,88	6,36E-04	Upf0503 protein chloroplastic-	UPF0503 protein At3g09070%2C chloroplastic
Solyc04g005700.2	0,87	1,33E-05	Kirola	Major latex-like protein
Solyc02g084950.2	0,87	5,03E-05	Salicylate o-methyltransferase	Carboxyl methyltransferase 4
Solyc03g064010.2	0,87	9,68E-05	Probable inactive leucine-rich repeat receptor-like protein kinase at1g66830	Receptor like kinase%2C RLK
Solyc01g094750.2	0,87	1,07E-04	Cytochrome p450 86a8-	Cytochrome P450
Solyc03g083350.2	0,87	1,19E-03	Phosphatidylinositol 4-kinase gamma 3	Ubiquitin
Solyc04g015030.2	0,87	9,67E-06	Neurofilament medium polypeptide-like	Metal ion binding protein
Solyc03g031910.2	0,87	1,73E-03	P-loop containing nucleoside triphosphate hydrolases superfamily	Helicase sen1
Solyc05g013010.2	0,87	6,41E-04	Cytosolic sulfotransferase 5-	Sulfotransferase family protein

Solyc03g115050.2	0,87	2,88E-03	Replication protein a 70 kda dna-binding subunit b	Single-stranded DNA-binding replication protein A large subunit
Solyc05g010320.2	0,87	2,14E-03	Chalcone isomerase	Chalcone--flavonone isomerase
Solyc04g074990.2	0,87	9,64E-05	Zinc-finger homeodomain protein 2-	Zinc finger-homeodomain protein 1 (Fragment)
Solyc09g082510.2	0,87	2,11E-04	Intracellular protein transport protein uso1-	Kinase interacting family protein
Solyc04g082950.2	0,87	1,00E-03	PREDICTED: uncharacterized protein LOC101247215	Unknown Protein
Solyc03g111680.2	0,86	4,59E-04	Protein stichel-	DNA polymerase III gamma/tau subunit
Solyc01g079110.2	0,86	2,25E-03	Histone	Histone H3
Solyc11g066130.1	0,86	8,26E-04	Osmotin-like protein	Thaumatin-like protein
Solyc02g068070.2	0,86	2,89E-03	Triacylglycerol lipase 2-	Lipase
Solyc05g012950.1	0,86	1,48E-03	Cytosolic sulfotransferase 5-like	Sulfotransferase family protein
Solyc06g064820.2	0,86	1,39E-03	Gdsl esterase lipase at1g71691-	GDSL esterase/lipase At1g71691
Solyc02g093100.2	0,86	9,89E-04	Probable inactive receptor kinase at5g67200	Receptor like kinase%2C RLK
Solyc02g090580.2	0,85	8,70E-05	Kinesin-like protein kif11	Os03g0859900 protein (Fragment)
Solyc04g008650.2	0,85	1,11E-03	Inactive leucine-rich repeat receptor-like serine threonine-protein kinase at1g60630	Receptor like kinase%2C RLK
Solyc04g015470.2	0,85	3,61E-04	Phosphatidylinositol 4-phosphate 5-kinase 1	Phosphatidylinositol-4-phosphate 5-kinase family protein
Solyc05g049980.2	0,85	1,36E-05	Probable polygalacturonase	Glycoside hydrolase family 28 protein/polygalacturonase family protein
Solyc04g008230.2	0,85	9,30E-05	Polygalacturonase at1g48100	Polygalacturonase
Solyc09g007360.2	0,85	1,69E-03	Interactor of constitutive active rops chloroplastic-like isoform x1	Interactor of constitutive active ROPs 3
Solyc02g071710.2	0,85	7,33E-04	Gdsl esterase lipase at1g29670-	GDSL esterase/lipase At1g29670
Solyc05g005870.2	0,85	1,18E-03	Wat1-related protein at1g70260-	Nodulin MtN21 family protein
Solyc05g013220.2	0,85	2,97E-04	3-ketoacyl- synthase 19-	Fatty acid elongase 3-ketoacyl-CoA synthase
Solyc01g080290.2	0,85	1,88E-03	Awpm-19-like protein	Plasma membrane associated protein-like
Solyc05g009990.2	0,84	3,11E-05	Piriformospora indica-insensitive protein 2-	LRR receptor-like serine/threonine-protein kinase%2C RLP
Solyc02g085110.2	0,84	1,58E-03	Laccase-11-	Laccase
Solyc05g009660.2	0,84	8,64E-04	Transcription factor hbp-1b -	BZIP transcription factor
Solyc10g084970.1	0,84	4,88E-05	PREDICTED: uncharacterized protein LOC101266378	Unknown Protein
Solyc06g009780.2	0,83	5,58E-05	Kinesin-4	Kinesin
Solyc08g014430.2	0,83	5,81E-04	Formin-like protein 1	Formin 3
Solyc05g006020.2	0,83	2,02E-03	Nucleobase-ascorbate transporter 7	Nucleobase ascorbate transporter
Solyc10g079090.1	0,83	1,15E-03	Chaperone protein dnaj 6-	Chaperone protein dnaJ 6
Solyc08g008610.2	0,83	1,95E-03	Alpha beta-hydrolases superfamily protein	Hydrolase alpha/beta fold family protein
Solyc08g078520.2	0,83	4,65E-04	PREDICTED: uncharacterized protein LOC101258981	Os03g0859900 protein (Fragment)
Solyc05g014690.1	0,82	2,69E-03	Atp-dependent dna helicase q-	ATP-dependent DNA helicase

Solyc03g113450.2	0,82	8,43E-04	Lrr receptor-like serine threonine-protein kinase fei 2	Receptor like kinase%2C RLK
Solyc02g091890.1	0,82	9,23E-04	Dentin sialophosphoprotein	MRNA complete cds clone RAFL24-22-E06
Solyc01g107800.2	0,82	2,24E-03	Protein irx15--	Expressed protein (Fragment)
Solyc06g075220.1	0,82	2,63E-04	Fasciclin-like arabinogalactan protein 11	Fasciclin-like arabinogalactan protein 5
Solyc03g112620.2	0,82	6,70E-04	PREDICTED: uncharacterized protein LOC101258936	Carboxyl-terminal proteinase
Solyc02g088820.2	0,82	2,58E-04	Unknown Protein	Serine carboxypeptidase K10B2.2
Solyc02g082260.2	0,82	2,23E-03	3-hydroxy-3-methylglutaryl-coenzyme a reductase 1	Hydroxy-methylglutaryl-coenzyme A reductase
Solyc04g045530.2	0,82	2,22E-03	Probable dna primase large subunit	DNA primase large subunit
Solyc01g103530.2	0,81	2,71E-04	Leucine-rich repeat receptor- serine threonine-protein kinase bam3	Receptor like kinase%2C RLK
Solyc02g080880.2	0,81	1,13E-04	Aspartic proteinase	Aspartic proteinase
Solyc05g007930.2	0,81	3,98E-04	Beta- -galactosyltransferase 15	Beta-1 3-galactosyltransferase-like protein
Solyc07g053950.1	0,81	6,03E-04	PREDICTED: uncharacterized protein LOC104648387	Unknown Protein
Solyc08g079740.2	0,81	2,79E-04	Probable lrr receptor-like serine threonine-protein kinase at1g12460	Receptor like kinase%2C RLK
Solyc06g048620.2	0,81	1,89E-04	Probably inactive leucine-rich repeat receptor-like protein kinase at3g28040	Receptor like kinase%2C RLK
Solyc01g065500.2	0,81	2,88E-03	Protein quirky isoform x2	Phosphoribosylanthranilate transferase (Fragment)
Solyc07g049500.2	0,80	9,75E-04	Protein argonaute 16	Argonaute 4-like protein
Solyc03g111820.2	0,80	4,80E-04	Sieve element occlusion a	Sieve element-occluding protein 3
Solyc01g096940.2	0,80	2,10E-05	Probable inactive leucine-rich repeat receptor-like protein kinase at3g03770	Receptor like kinase%2C RLK
Solyc01g006540.2	0,80	6,75E-05	Linoleate 13s-lipoxygenase 2- chloroplastic-	Lipoxygenase
Solyc02g084610.1	0,80	2,39E-04	Probable lrr receptor-like serine threonine-protein kinase at4g36180	LRR receptor-like serine/threonine-protein kinase%2C RLP
Solyc04g077190.2	0,80	3,20E-04	Glycosyl hydrolase family 10 protein carbohydrate-binding domain-containing protein isoform 1	Endo-1 4-beta-xylanase
Solyc01g096190.2	0,79	6,77E-05	Calcium-transporting endoplasmic reticulum-type	Calcium-transporting ATPase
Solyc08g023280.2	0,79	1,53E-03	Protein breast cancer susceptibility 1 homolog	Tripartite motif-containing 22 (Predicted)
Solyc10g007870.2	0,79	4,16E-05	Thionin-like protein	Tumor-related protein
Solyc04g081240.2	0,79	5,43E-04	Auxin response factor 5	Auxin response factor 5
Solyc11g007330.1	0,79	1,90E-03	Rab6-interacting golgin-	cDNA clone J033118E13 full insert sequence
Solyc08g079090.2	0,79	2,51E-03	Monocopper oxidase-like protein sku5	Laccase-22
Solyc03g007800.2	0,79	2,13E-04	Protein timeless homolog	Topoisomerase 1-associated factor 1
Solyc02g071820.2	0,79	1,01E-03	Probable lrr receptor-like serine threonine-protein kinase at1g07650	Receptor like kinase%2C RLK
Solyc06g071330.2	0,78	1,17E-03	Nucleobase-ascorbate transporter 6	Nucleobase ascorbate transporter
Solyc01g090440.2	0,78	1,88E-04	Peptidyl-prolyl cis-trans isomerase fkbp20-2	Unknown Protein

Solyc12g008530.1	0,78	4,24E-05	Probable pectinesterase 53	Pectinesterase
Solyc02g070780.2	0,78	6,34E-04	Dna replication licensing factor mcm3 homolog 2 isoform x2	DNA replication licensing factor MCM3
Solyc03g097380.2	0,78	5,80E-05	Neurofilament medium polypeptide-	Heavy metal-associated domain containing protein expressed
Solyc09g092740.2	0,78	1,47E-04	Fam10 family protein at4g22670-	Unknown Protein
Solyc01g111570.2	0,78	2,32E-03	Probable receptor-like serine threonine-protein kinase at5g57670	Receptor-like kinase
Solyc02g065240.2	0,78	1,98E-04	Salicylic acid-binding protein 2-	Hydrolase alpha/beta fold family protein
Solyc05g012790.2	0,77	8,53E-04	Probable protein s-acyltransferase 22	Palmitoyltransferase erf2
Solyc01g079240.2	0,77	2,17E-03	Unknown Protein	Long-chain-fatty-acid--CoA ligase family protein
Solyc03g120380.2	0,77	3,02E-04	Auxin-induced protein aux22-	Auxin response factor 9
Solyc03g082860.2	0,77	1,96E-03	Histone-lysine n-methyltransferase atxr6	Histone-lysine N-methyltransferase
Solyc09g011050.2	0,77	2,88E-03	Laccase-17-	Laccase
Solyc09g074930.2	0,77	4,56E-04	Stress-related protein	REF-like stress related protein 1
Solyc04g078810.2	0,77	1,47E-03	Remorin family protein isoform 2	Remorin
Solyc12g057080.1	0,77	2,04E-03	7-deoxyloganetin glucosyltransferase-	UDP-glucuronosyltransferase
Solyc05g009820.2	0,76	2,85E-04	Probable galacturonosyltransferase-like 3	Glycosyltransferase family GT8 protein
Solyc02g090070.2	0,76	1,14E-03	Btb poz domain-containing protein at5g66560	Phototropic-responsive NPH3 family protein
Solyc09g092510.2	0,76	8,13E-04	PREDICTED: uncharacterized protein LOC101249961 isoform X1	Unknown Protein
Solyc03g121610.2	0,76	1,84E-03	Receptor-like serine threonine-protein kinase ale2	Receptor-like kinase
Solyc02g030480.2	0,76	1,84E-03	Probable cinnamyl alcohol dehydrogenase 6	Cinnamyl alcohol dehydrogenase-like protein
Solyc11g013270.1	0,76	7,96E-04	PREDICTED: uncharacterized protein At1g04910-	Os01g0841200 protein (Fragment)
Solyc06g008510.2	0,75	8,60E-04	Cdt1-like protein chloroplastic	CDT1a protein
Solyc12g044840.1	0,75	2,10E-03	Inactive protein kinase selmodraft_444075	Receptor-like kinase
Solyc01g079500.2	0,75	1,13E-03	Dna replication licensing factor mcm7	DNA replication licensing factor
Solyc01g006370.2	0,75	2,73E-03	Callose synthase 3	Glucan synthase like 3
Solyc06g069820.2	0,75	1,28E-03	PREDICTED: uncharacterized protein LOC101254212	Unknown Protein
Solyc08g080780.2	0,74	2,43E-04	Unknown Protein	SKIP interacting protein 24 (Fragment)
Solyc02g086650.2	0,74	1,28E-03	Phosphoenolpyruvate phosphate translocator chloroplastic-	Glucose-6-phosphate/phosphate translocator 2
Solyc10g080090.1	0,74	9,71E-04	Zinc finger bed domain-containing protein daysleeper-	HAT family dimerisation domain containing protein expressed
Solyc03g005460.2	0,74	1,33E-03	Swi snf-related matrix-associated actin-dependent regulator of chromatin subfamily a member 3-	DNA helicase
Solyc03g078780.1	0,74	2,90E-03	Udp-glycosyltransferase 76f1-	UDP-glucosyltransferase
Solyc04g078750.2	0,73	2,40E-03	PREDICTED: uncharacterized protein LOC101250111 isoform X1	Harpin-induced protein
Solyc12g056300.1	0,73	4,92E-04	Probable lrr receptor-like serine threonine-protein kinase at1g63430	Receptor like kinase%2C RLK
Solyc07g047830.2	0,73	9,68E-04	PREDICTED: uncharacterized protein LOC101254220	Bzip-like transcription factor-like

Solyc10g085070.1	0,73	2,09E-03	Upf0503 protein chloroplastic-	UPF0503 protein At3g09070%2C chloroplastic
Solyc02g093300.2	0,73	5,95E-04	Dna polymerase alpha catalytic subunit	DNA polymerase
Solyc09g092460.2	0,73	6,03E-04	Probable receptor protein kinase tmk1	Receptor-like kinase
Solyc12g014140.1	0,73	1,38E-04	Transcription factor tcp4-	Transcription factor CYCLOIDEA (Fragment)
Solyc08g081120.2	0,73	5,28E-04	Kinesin kp1	Kinesin-like protein 73641-79546
Solyc06g048950.2	0,73	9,19E-04	Probably inactive leucine-rich repeat receptor-like protein kinase at3g28040	Receptor like kinase%2C RLK
Solyc08g067240.2	0,73	8,19E-04	Brct domain-containing dna repair protein	DNA topoisomerase 2-binding protein 1
Solyc05g051640.2	0,73	1,29E-03	Leucine-rich repeat receptor-like protein kinase tdr	Receptor like kinase%2C RLK
Solyc03g093460.2	0,73	1,78E-03	Kinase-like protein tmkl1	Receptor-like kinase
Solyc07g049550.2	0,73	2,25E-04	1-aminocyclopropane-1-carboxylate oxidase	1-aminocyclopropane-1-carboxylate oxidase
Solyc11g071850.1	0,72	2,52E-04	PREDICTED: uncharacterized protein LOC101260304	AT5G22070 protein (Fragment)
Solyc07g007980.2	0,72	7,18E-04	Probable receptor-like protein kinase at5g15080	ATP binding / serine-threonine kinase
Solyc10g011820.2	0,72	7,12E-04	Delta -fatty-acid desaturase-	Delta-6 desaturase
Solyc10g085850.1	0,72	1,75E-03	Tpsi1	TPSI1
Solyc04g082710.2	0,72	2,69E-04	Xylem cysteine proteinase 1-	Cathepsin B-like cysteine proteinase 3
Solyc07g018240.1	0,71	7,92E-04	Elongation of fatty acids protein 3-	Elongation of very long chain fatty acids protein 4
Solyc04g073970.2	0,71	1,35E-03	PREDICTED: uncharacterized protein LOC101251468	cDNA clone J033025P19 full insert sequence
Solyc05g014540.2	0,71	7,94E-04	Dna polymerase alpha subunit b	DNA polymerase alpha subunit B family
Solyc01g112260.2	0,70	2,62E-03	PREDICTED: uncharacterized protein LOC101258903	Unknown Protein
Solyc07g018300.2	0,70	1,50E-03	Replication protein a 32 kda subunit a-	Single-stranded DNA binding protein p30 subunit
Solyc10g081250.1	0,70	1,36E-03	Dna polymerase delta catalytic subunit	DNA polymerase
Solyc07g042390.1	0,70	1,31E-03	21 kda	Pectinesterase
Solyc04g079340.2	0,70	6,92E-04	PREDICTED: uncharacterized protein LOC101262306 isoform X1	Os03g0859900 protein (Fragment)
Solyc12g044310.1	0,70	1,57E-03	Protein nrt1 ptr family	Solute carrier family 15 member 4
Solyc09g090020.2	0,69	7,01E-04	Germin-like protein subfamily 1 member 17	Germin-like protein 5
Solyc10g005960.1	0,69	1,38E-03	Fasciclin-like arabinogalactan protein 1	Fasciclin-like arabinogalactan protein 10
Solyc06g074850.2	0,69	1,83E-03	Serine carboxypeptidase-	Serine carboxypeptidase
Solyc08g079650.2	0,69	7,23E-04	Amino acid binding	ACT domain containing protein expressed
Solyc08g061560.2	0,69	6,62E-04	Lrr receptor-like serine threonine-protein kinase erecta	Receptor like kinase%2C RLK
Solyc05g026240.1	0,69	1,96E-03	Leucine-rich repeat extensin- protein 4	LRR receptor-like serine/threonine-protein kinase%2C RLP
Solyc04g082110.2	0,69	2,01E-03	Rop guanine nucleotide exchange factor 1-	Rop guanine nucleotide exchange factor 1
Solyc09g011960.1	0,69	1,31E-03	Laccase-17	Laccase
Solyc01g102390.2	0,68	3,96E-04	Nectarin-1	Germin-like protein

Solyc07g008670.2	0,68	1,71E-03	Protein longifolia 1-	AT1G74160 protein (Fragment)
Solyc02g024070.2	0,68	1,74E-03	Homeobox-leucine zipper protein athb-14-	Class III homeodomain-leucine zipper
Solyc05g005170.2	0,68	4,73E-04	Polygalacturonase at1g48100-	Polygalacturonase 2
Solyc06g068770.2	0,68	9,54E-04	Probable beta- -xylosyltransferase irx10l	Exostosin-like glycosyltransferase
Solyc10g074920.1	0,68	4,81E-04	Mannan endo- -beta-mannosidase 6 isoform x1	Mannan endo-1 4-beta-mannosidase
Solyc10g083670.1	0,68	2,58E-03	Glucomannan 4-beta-mannosyltransferase 9	Cellulose synthase-like C2 glycosyltransferase family 2
Solyc09g075360.2	0,67	2,64E-03	Endoglucanase 17	Endoglucanase 1
Solyc08g066490.2	0,67	2,41E-03	Probably inactive leucine-rich repeat receptor-like protein kinase at2g25790	Receptor like kinase%2C RLK
Solyc05g013690.2	0,67	1,77E-03	Gdsl esterase lipase at3g26430-	GDSL esterase/lipase At3g26430
Solyc09g083400.2	0,67	2,72E-03	Protein wvd2-like 1 isoform x1	Os02g0200800 protein (Fragment)
Solyc01g096040.2	0,67	2,29E-03	Protein aspartic protease in guard cell 2	Aspartic proteinase nepenthesin I
Solyc11g072490.1	0,67	1,50E-03	Interactor of constitutive active rops 3-like isoform x1	Interactor of constitutive active ROPs 3
Solyc09g082500.2	0,66	1,37E-03	Protein tesmin tso1-like cxc 2 isoform x1	Tesmin/TSO1-like CXC domain containing protein expressed
Solyc11g044940.1	0,66	1,02E-03	Serine threonine-protein kinase-like protein acr4	Pto-like%2C Serine/threonine kinase protein%2C resistance protein
Solyc01g098740.2	0,66	1,34E-03	Pto-interacting protein 1	Receptor protein kinase-like protein
Solyc08g080720.2	0,66	2,87E-03	Selenoprotein h-	Selenoprotein H
Solyc01g110960.2	0,66	1,82E-03	Prefoldin chaperone subunit family	Glutamic acid-rich protein
Solyc02g072240.2	0,65	3,92E-04	Cellulose synthase a catalytic subunit 8	Cellulose synthase
Solyc07g062680.1	0,65	1,28E-03	Transcription factor tcp4-	Transcription factor CYCLOIDEA (Fragment)
Solyc12g008490.1	0,65	1,57E-03	Nucleotide-diphospho-sugar transferases superfamily protein isoform 1	Ceramide glucosyltransferase
Solyc06g072700.2	0,64	1,21E-03	Neurofilament medium polypeptide-	Metal ion binding protein
Solyc02g084390.2	0,64	1,45E-03	Kinesin-like protein nack1	Kinesin like protein
Solyc03g096800.2	0,64	1,69E-03	Membrane protein of er body-like protein isoform x1	At5g24290-like protein (Fragment)
Solyc12g088760.1	0,63	2,05E-03	Subtilisin-like protease	Subtilisin-like protease
Solyc02g092670.1	0,63	9,98E-04	Subtilisin-like protease	Subtilisin-like protease
Solyc09g011160.2	0,62	2,83E-03	Ultraviolet-b receptor uvr8-like isoform x1	Regulator of chromosome condensation RCC1
Solyc05g010400.2	0,62	1,86E-03	Protein nsp-interacting kinase 2-	Receptor like kinase%2C RLK
Solyc03g019890.2	0,61	2,77E-03	Beta-galactosidase 10	Beta-galactosidase
Solyc07g021700.2	0,61	2,78E-03	Pollen-specific protein sf21-	N-myc downstream regulated (Fragment)
Solyc04g078700.2	0,61	2,21E-03	Probable serine threonine-protein kinase at1g01540	Receptor-like protein kinase
Solyc01g110580.2	0,61	2,73E-03	Auxin-induced protein 15a-	Auxin-induced SAUR-like protein
Solyc09g097890.2	0,61	2,03E-03	Cytochrome b561 and domon domain-containing protein at3g25290-	Membrane protein

Solyc05g009680.1	0,60	2,82E-03	Protein aspartic protease in guard cell 1	Aspartic proteinase nepenthesin I
Solyc10g086660.1	0,60	1,70E-03	Rop guanine nucleotide exchange factor 7-	Rop guanine nucleotide exchange factor 1
Solyc04g009180.1	0,60	1,95E-03	Transcription factor tcp7-	TCP family transcription factor
Solyc01g107650.2	0,59	2,24E-03	Probable lrr receptor-like serine threonine-protein kinase at4g37250	Receptor like kinase%2C RLK
Solyc03g110880.2	0,59	2,81E-03	Unknown Protein	DNA-directed RNA polymerase
Solyc07g064380.2	5,45	3,06E-05	Serine threonine-protein phosphatase 7 long form homolog	Serine/threonine-protein phosphatase 7 long form homolog
Solyc10g054900.1	4,99	2,46E-03	Proline-rich protein 4-	Proline-rich protein
Solyc07g040960.1	4,30	2,68E-04	Nuclease harbi1	Os07g0175100 protein (Fragment)
Solyc10g018190.1	4,21	1,12E-03	Hyoscyamine 6-dioxygenase-	1-aminocyclopropane-1-carboxylate oxidase
Solyc06g062560.1	3,76	1,83E-04	Inorganic pyrophosphatase 1-	Phosphatase
Solyc01g090890.2	3,40	8,46E-05	Spx domain-containing protein 3	Xenotropic and polytropic retrovirus receptor
Solyc01g091590.2	3,34	1,34E-03	Bon1-associated protein 2-	SRC2 protein
Solyc08g067230.2	3,22	2,88E-03	Type ii mads-box transcription partial	MADS box transcription factor
Solyc04g074420.1	2,90	1,24E-05	Unknown Protein	Phi-1 protein (Fragment)
Solyc03g082430.1	2,84	2,50E-04	Growth-regulating factor 7-like isoform x3	Growth-regulating factor 4
Solyc03g093560.1	2,76	8,10E-04	Ethylene-responsive transcription factor 5-	Ethylene-responsive transcription factor 2
Solyc06g074030.1	2,70	1,26E-04	Probable ccr4-associated factor 1 homolog 11	CCR4-NOT transcription complex subunit 7
Solyc04g074440.1	2,57	1,25E-04	Protein exordium-	Os06g0220000 protein (Fragment)
Solyc10g006700.1	2,47	3,47E-04	Calcium-binding protein pbp1-	Calcium-binding EF hand family protein (Fragment)
Solyc06g035530.2	2,37	1,80E-06	Gibberellin 20 oxidase 1-	Gibberellin 20-oxidase-2
Solyc01g009160.2	2,33	2,00E-04	Protein yls9	Harpin-induced protein-like (Fragment)
Solyc04g077980.1	2,19	9,14E-04	Zinc finger protein zat10-	Zinc-finger protein
Solyc04g074430.1	2,19	9,80E-05	Protein exordium-	Phi-1 protein (Fragment)
Solyc08g083050.1	2,17	1,81E-03	PREDICTED: uncharacterized protein At1g01500	Unknown Protein
Solyc08g066890.2	2,07	4,04E-04	Bark storage protein a	Unknown Protein
Solyc10g055740.1	1,98	2,59E-03	Lysine histidine transporter-	Lysine/histidine transporter
Solyc08g068600.2	1,84	1,99E-04	Histidine decarboxylase-	Decarboxylase family protein
Solyc04g074450.1	1,82	1,42E-04	Protein exordium-	Phi-1 protein (Fragment)
Solyc06g007180.2	1,81	2,30E-03	Asparagine synthetase	Asparagine synthase (Glutamine-hydrolyzing)
Solyc06g062540.2	1,77	5,22E-04	Inorganic pyrophosphatase 1-	Phosphatase
Solyc08g066880.2	1,69	1,49E-03	Bark storage protein a-	5%26apos-methylthioadenosine/S-adenosylhomocysteine nucleosidase
Solyc00g206460.1	1,68	3,34E-04	Unknown Protein	Os06g0220000 protein (Fragment)
Solyc01g007010.2	1,55	2,05E-03	E3 ubiquitin-protein ligase pub22-	U-box domain-containing protein

Solyc10g006660.2	1,54	2,47E-03	Calcium-binding protein pbp1-	Calcium-binding EF hand family protein (Fragment)
Solyc04g024840.2	1,51	1,25E-03	Unknown Protein	GDSL esterase/lipase 1
Solyc01g106910.2	1,49	1,73E-05	PREDICTED: putative uncharacterized protein DDB_G0284695	Unknown Protein
Solyc03g034390.1	1,44	1,67E-04	Non-specific lipid-transfer protein 2-	Lipid transfer protein
Solyc03g114560.2	1,42	1,27E-05	Strictosidine synthase 3-	Strictosidine synthase family protein
Solyc10g083170.1	1,42	5,99E-05	Secoisolariciresinol dehydrogenase-	2%2C5-dichloro-2%2C5-cyclohexadiene-1%2C4-diol dehydrogenase
Solyc12g013700.1	1,41	1,55E-03	Stem-specific protein tsjt1-	Aluminum-induced protein-like protein
Solyc05g005670.1	1,40	1,89E-03	U-box domain-containing protein 19-	U-box domain-containing protein
Solyc11g072980.1	1,38	2,44E-05	3-ketoacyl- synthase 3-	3-ketoacyl-CoA synthase 6
Solyc04g071030.1	1,36	1,17E-04	U-box domain-containing protein 28-	U-box domain-containing protein
Solyc07g056400.1	1,32	1,13E-03	Serine threonine-protein kinase wag1-	Ribosomal protein S6 kinase alpha-6
Solyc09g072630.2	1,31	1,41E-03	Piriformospora indica-insensitive protein 2	LRR receptor-like serine/threonine-protein kinase%2C RLP
Solyc09g015770.2	1,24	1,88E-03	Probable wrky transcription factor 70	WRKY transcription factor 6
Solyc12g010800.1	1,23	1,97E-05	Basic leucine zipper 61-	BZIP transcription factor family protein
Solyc10g008930.1	1,20	5,20E-05	Glutaredoxin-c9-	Glutaredoxin
Solyc08g061910.2	1,19	1,08E-05	Trihelix transcription factor gt-2-	Unknown Protein
Solyc12g087940.1	1,17	3,50E-05	Aspartic proteinase nepenthesin-1-	Aspartic proteinase nepenthesin-1
Solyc01g089850.2	1,17	6,56E-05	Cyclin-u4-1	Cyclin-dependent protein kinase regulator Pho80
Solyc04g074410.1	1,16	3,16E-04	Protein exordium-	Os06g0220000 protein (Fragment)
Solyc03g093610.1	1,15	4,39E-04	Ethylene-responsive transcription factor 1	Ethylene responsive transcription factor 1b
Solyc04g082270.2	1,10	8,61E-04	PREDICTED: uncharacterized protein LOC101254897	CM0216.210.nc protein
Solyc09g065660.2	1,10	1,46E-04	Heat stress transcription factor a-7a isoform x6	Heat stress transcription factor A3
Solyc01g079580.2	1,07	1,07E-04	Heat shock protein with tetratricopeptide repeat isoform 1	DNAJ heat shock N-terminal domain-containing protein
Solyc06g066160.2	1,04	9,24E-04	Bifunctional pinoresinol-lariciresinol reductase 2-	Pinoresinol-lariciresinol reductase
Solyc12g089050.1	1,01	1,03E-03	Acyl- --sterol o-acyltransferase 1-	Wax synthase isoform 1
Solyc03g097170.2	1,00	4,68E-04	Cinnamoyl- reductase 1-	Cinnamoyl-CoA reductase-like protein
Solyc07g053450.2	0,99	1,32E-03	Basic leucine zipper 61-	BZIP transcription factor family protein
Solyc11g006650.1	0,98	3,39E-04	Double clp-n motif-containing p-loop nucleoside triphosphate hydrolases superfamily	Heat shock protein 101
Solyc10g047530.1	0,97	2,40E-03	Root phototropism protein 3-	Phototropic-responsive NPH3 family protein
Solyc02g086840.2	0,96	1,33E-04	Tetratricopeptide repeat protein 28-	Kinesin light chain-like protein
Solyc02g079490.2	0,96	3,33E-04	Shikimate o-hydroxycinnamoyltransferase-	Hydroxycinnamoyl-CoA shikimate/quinate hydroxycinnamoyl transferase
Solyc01g095100.2	0,91	1,90E-03	Wrky transcription factor 22-	WRKY transcription factor 23
Solyc09g092520.2	0,90	1,27E-03	Brassinosteroid-regulated protein bru1-	Xyloglucan endotransglucosylase/hydrolase 8

Solyc10g074540.1	0,87	2,43E-04	Protein exordium-	Expressed protein (Fragment)
Solyc03g123620.2	0,84	2,65E-03	Pectinesterase 3	Pectinesterase
Solyc08g076820.2	0,82	5,71E-05	Transcription factor bhlh71-	BHLH transcription factor
Solyc07g056410.2	0,81	1,66E-03	Leucine-rich repeat receptor- serine threonine-protein kinase at1g17230	Receptor like kinase%2C RLK
Solyc04g008500.2	0,81	3,76E-04	Protein indeterminate-domain chloroplastic-	C2H2L domain class transcription factor
Solyc07g063850.2	0,79	1,91E-03	Indole-3-acetic acid-amido synthetase	Indole-3-acetic acid-amido synthetase GH3.8
Solyc01g106690.2	0,79	7,06E-04	Formin-like protein 18	Unknown Protein
Solyc09g015040.1	0,76	1,94E-03	Unknown Protein	Os08g0119500 protein (Fragment)
Solyc10g008490.2	0,75	1,09E-03	Probable protein phosphatase 2c 52	Protein phosphatase 2c
Solyc04g082420.2	0,74	1,55E-03	Btb poz domain-containing protein at2g30600 isoform x2	BTB/POZ domain-containing protein
Solyc03g118310.2	0,73	8,42E-04	Transcription factor ice1-	BHLH transcription factor
Solyc02g092930.1	0,72	1,46E-03	Transcription factor myb44-	MYB transcription factor
Solyc11g069660.1	0,72	1,39E-03	Disease resistance partial	Nbs-lrr%2C resistance protein
Solyc05g005000.2	0,71	1,91E-03	PREDICTED: uncharacterized protein LOC101268569 isoform X1	Lipase
Solyc06g050840.2	0,71	1,33E-03	Transcription factor scream2-like isoform x1	DNA binding protein
Solyc03g098290.2	0,67	1,53E-03	Sucrose synthase 6-	Sucrose synthase
Solyc09g011690.2	0,65	1,85E-03	PREDICTED: uncharacterized protein LOC101263742	Unknown Protein
Solyc07g062580.2	0,62	2,59E-03	Tpr repeat-containing thioredoxin ttl1	DnaJ homolog subfamily C member 7
Solyc07g006710.1	0,60	2,10E-03	Pathogenesis-related protein pr-1-	Pathogenesis-related protein PR-1

Table 2: List of DOWN-regulated genes; the genes description were obtained according to Blast2GO and AgriGO annotations

Locus	logFC	PValue	Blast2GO annotation	AgriGO annotation
Solyc04g052890.1	-6,68	7,83E-05	Auxin-induced protein 6b-	Auxin-responsive protein
Solyc02g005050.2	-4,77	6,65E-04	Predicted: uncharacterized protein LOC101251233	Unknown Protein
Solyc09g018200.1	-4,58	1,02E-03	Transcription repressor ofp1	Plant-specific domain TIGR01568 family protein
Solyc08g013950.1	-4,11	4,84E-06	Unknown Protein	Unknown Protein
Solyc02g061780.2	-3,82	1,43E-25	Nac domain-containing protein 94	NAC domain transcription factor
Solyc04g011790.1	-3,59	7,63E-06	Monothiol glutaredoxin-s1-	Glutaredoxin
Solyc09g008750.1	-3,53	9,44E-09	Vq motif-containing protein 29-	Unknown Protein
Solyc02g079480.1	-3,35	1,31E-07	Tetrahydrocannabinolic acid synthase-	FAD-binding domain-containing protein
Solyc05g052670.1	-3,00	2,81E-19	Uncharacterized acetyltransferase at3g50280-	N-hydroxycinnamoyl/benzoyltransferase 1
Solyc06g051860.1	-2,92	6,22E-07	Inorganic phosphate transporter 1-11	Inorganic phosphate transporter 6
Solyc03g116620.2	-2,82	1,73E-04	Phospholipase d alpha 1	Phospholipase D
Solyc09g007010.1	-2,74	2,62E-35	Pathogenesis-related leaf protein 4	Pathogenesis related protein PR-1
Solyc12g094610.1	-2,73	2,93E-04	U-box domain-containing protein 15	U-box domain-containing protein 15
Solyc03g033750.1	-2,65	1,45E-04	Probable mitochondrial chaperone bcs1-a	BCS1 protein-like protein
Solyc08g080640.1	-2,58	6,39E-19	Osmotin-like protein	Osmotin-like protein (Fragment)
Solyc08g080650.1	-2,53	2,63E-25	Osmotin-like protein	Osmotin-like protein (Fragment)
Solyc00g174340.1	-2,51	5,88E-27	Unknown Protein	Pathogenesis-related protein 1b
Solyc05g009170.1	-2,49	6,69E-05	Zinc finger protein 6-	Zinc finger protein 6
Solyc02g086700.2	-2,47	2,51E-16	Glucan endo- -beta-glucosidase	Beta-1 3-glucanase
Solyc07g049530.2	-2,40	6,25E-28	1-aminocyclopropane-1-carboxylate oxidase 1	1-aminocyclopropane-1-carboxylate oxidase
Solyc09g010990.2	-2,35	1,14E-04	Laccase-17-	Laccase
Solyc08g081470.2	-2,33	6,95E-06	Protein spiral1-	Nitrilase-associated protein
Solyc00g174330.2	-2,32	7,49E-22	Unknown Protein	Pathogenesis related protein PR-1
Solyc02g082920.2	-2,29	1,66E-19	Class ii chitinase	Endochitinase (Chitinase)

Solyc09g089930.1	-2,27	1,59E-16	Ethylene-responsive transcription factor 1b	Ethylene responsive transcription factor 1a
Solyc02g064690.2	-2,26	3,36E-09	Probable n-acetyltransferase hls1	Acetyltransferase-like protein
Solyc01g087810.2	-2,14	8,52E-18	Subtilisin-like protease	Subtilisin-like protease
Solyc09g005730.2	-2,14	1,89E-06	Math and lrr domain-containing protein pfe0570w	Plant-specific domain TIGR01589 family protein
Solyc01g087820.2	-2,11	3,34E-19	Subtilisin-like protease	Subtilisin-like protease
Solyc03g025670.2	-2,10	5,24E-18	PREDICTED: uncharacterized protein LOC101252465	PAR-1c protein
Solyc10g044680.1	-2,09	4,37E-04	Transcription factor myb86-	Myb-like transcription factor
Solyc10g075150.1	-2,08	2,09E-23	Non-specific lipid-transfer protein 2	Non-specific lipid-transfer protein
Solyc01g087840.2	-2,08	3,83E-09	Subtilisin-like protease	Subtilisin-like protease
Solyc03g119390.2	-2,01	2,08E-04	Transcription factor bee 1-	Transcription factor
Solyc04g040180.2	-2,01	3,00E-04	Methyltransferase ddb_g0268948	S-adenosylmethionine-dependent methyltransferase (Fragment)
Solyc01g008620.2	-1,98	1,25E-14	3)-beta-glucan endohydrolase short	Beta-1 3-glucanase
Solyc08g006470.2	-1,98	6,07E-06	Zinc finger protein 622	Zinc finger family protein
Solyc03g120110.2	-1,98	2,03E-06	G-type lectin s-receptor-like serine threonine-protein kinase ces101	Serine/threonine kinase receptor
Solyc11g032220.1	-1,97	7,62E-10	12-oxophytodienoate reductase 11	NADPH dehydrogenase 1
Solyc06g008620.1	-1,95	7,59E-11	Isoform 1	Protein tolB
Solyc04g007980.2	-1,93	2,18E-15	1-aminocyclopropane-1-carboxylate oxidase homolog 4	1-aminocyclopropane-1-carboxylate oxidase
Solyc09g090970.2	-1,89	2,43E-04	Pathogenesis-related protein sth-2	Major allergen Mal d 1
Solyc08g005510.1	-1,89	5,15E-05	Tmv resistance protein	Tir-nbs-lrr%2C resistance protein
Solyc05g053600.2	-1,88	8,93E-09	Pleiotropic drug resistance protein 1	ATP-binding cassette transporter
Solyc03g098480.1	-1,85	2,74E-06	PREDICTED: uncharacterized protein LOC104089265	Unknown Protein
Solyc05g009040.2	-1,83	2,79E-04	Probable receptor-like protein kinase at1g67000-	Receptor-like protein kinase
Solyc10g075090.1	-1,83	5,89E-19	Non-specific lipid-transfer protein 2	Non-specific lipid-transfer protein
Solyc05g008250.1	-1,83	3,48E-08	Transcription factor myb3-	Myb-like transcription factor 6
Solyc12g011150.1	-1,82	5,28E-08	PREDICTED: uncharacterized protein LOC101254173	Unknown Protein
Solyc01g067460.1	-1,80	6,90E-13	Monothiol glutaredoxin-s2	Glutaredoxin family protein

Solyc08g078760.1	-1,78	3,19E-11	PREDICTED: uncharacterized protein LOC101253408	AT5g47580/MNJ7_17
Solyc07g053890.2	-1,76	2,18E-09	O-acyltransferase wsd1	O-acyltransferase WSD1
Solyc01g107780.2	-1,75	3,78E-08	Scopoletin glucosyltransferase-	UDP-glucosyltransferase family 1 protein
Solyc10g055800.1	-1,75	4,50E-11	Endochitinase 4	Chitinase
Solyc03g033840.2	-1,73	8,35E-08	Probable mitochondrial chaperone bcs1-a	26S protease regulatory subunit 6B homolog
Solyc04g079030.2	-1,73	3,61E-05	Udp-glycosyltransferase 79b6-	Anthocyanidin 3-O-glucosyltransferase
Solyc11g065940.1	-1,73	1,15E-15	Enth vhs family protein	Epsin 2-like protein (Fragment)
Solyc10g080670.1	-1,72	9,50E-12	PREDICTED: uncharacterized protein LOC101267365	Unknown Protein
Solyc10g055810.1	-1,71	8,38E-14	Endochitinase 4	Endochitinase (Chitinase)
Solyc02g077040.2	-1,71	4,67E-14	Senescence-specific cysteine protease sag39-	Cathepsin B-like cysteine proteinase 5
Solyc01g006550.2	-1,70	3,94E-09	Receptor-like protein 12 isoform x2	LRR receptor-like serine/threonine-protein kinase%2C RLP
Solyc05g052280.2	-1,69	1,69E-06	Peroxidase p7	Peroxidase
Solyc12g042480.1	-1,69	5,22E-10	Cytochrome p450 cyp736a12-	Cytochrome P450
Solyc09g057960.1	-1,66	2,52E-04	Cysteine-rich repeat secretory protein 55-	Cysteine-rich receptor-like protein kinase
Solyc08g005890.2	-1,66	2,97E-04	Uncharacterized acetyltransferase at3g50280-	Hydroxycinnamoyl transferase
Solyc01g097270.2	-1,64	7,89E-12	Wound-induced protein win2	Chitinase (Fragment)
Solyc04g080650.2	-1,64	7,72E-04	Abscisic acid 8 -hydroxylase 2	Cytochrome P450
Solyc01g098590.2	-1,63	1,40E-12	Broad-range acid phosphatase det1-	Phosphoglycerate mutase family protein
Solyc00g201160.2	-1,61	1,84E-03	Unknown Protein	Receptor protein kinase
Solyc02g068830.1	-1,59	1,38E-07	Probable lrr receptor-like serine threonine-protein kinase at3g47570	Receptor like kinase%2C RLK
Solyc01g009690.1	-1,59	1,95E-05	Receptor-like protein 12 isoform x1	LRR receptor-like serine/threonine-protein kinase%2C RLP
Solyc10g075070.1	-1,58	5,20E-10	Non-specific lipid-transfer protein 2-	Non-specific lipid-transfer protein
Solyc06g069070.1	-1,58	2,57E-08	Non-specific lipid-transfer protein 2-	Lipid transfer protein
Solyc07g043250.1	-1,58	5,61E-05	PREDICTED: uncharacterized protein LOC104648424	Unknown Protein
Solyc12g089130.1	-1,55	2,17E-04	Random slug protein 5	CRAL/TRIO domain containing protein expressed
Solyc11g011710.1	-1,52	7,53E-05	Auxin-induced protein 6b-	Auxin-responsive protein
Solyc08g079870.1	-1,52	1,16E-12	Subtilisin-like protease	Subtilisin-like protease

Solyc06g054090.1	-1,51	2,46E-04	Gcn5-related n-acetyltransferase family protein	Ribosomal-protein-alanine N-acetyltransferase
Solyc06g060590.2	-1,50	1,34E-07	Bidirectional sugar transporter sweet1-	Nodulin MtN3 family protein
Solyc03g120260.2	-1,49	2,04E-04	Beta subunit isoform 1	Coatomer beta%26apos subunit
Solyc01g097240.2	-1,48	1,22E-06	Chitinase hevein pr-4 wheatwin2	Pathogenesis-related protein 4B (Fragment)
Solyc12g088190.1	-1,46	3,87E-09	Amino acid permease 6-	Amino acid permease 6
Solyc10g083690.2	-1,45	1,17E-04	Cytochrome p450 76a2-	Cytochrome P450
Solyc08g079430.2	-1,44	1,40E-09	Primary amine oxidase-	Primary amine oxidase
Solyc09g097770.2	-1,44	2,22E-05	Tyrosine- and lysine-rich protein precursor	Cell wall protein
Solyc04g064530.1	-1,44	1,08E-08	PREDICTED: uncharacterized protein LOC101258062	Unknown Protein
Solyc01g067020.2	-1,42	6,15E-08	Probable inactive receptor kinase at1g48480	Receptor like kinase%2C RLK
Solyc02g076980.2	-1,41	1,91E-08	Cysteine protease	Cathepsin B-like cysteine proteinase
Solyc05g006990.2	-1,39	3,21E-07	Protein nrt1 ptr family -	Nitrate transporter
Solyc03g095650.2	-1,39	1,09E-12	Mlo1	MLO-like protein 17
Solyc11g017280.1	-1,38	2,93E-04	Leucine-rich repeat receptor-like tyrosine-protein kinase at2g41820	Receptor like kinase%2C RLK
Solyc01g006290.2	-1,38	1,47E-07	Lignin-forming anionic peroxidase-	Peroxidase
Solyc04g079420.2	-1,38	1,37E-09	Probable disease resistance protein at4g33300	Nbs-lrr%2C resistance protein
Solyc06g048410.2	-1,37	3,96E-08	Superoxide dismutase	Superoxide dismutase
Solyc01g005470.2	-1,37	3,17E-05	Protein plant cadmium resistance 2-	Cell number regulator 10
Solyc09g064940.2	-1,37	3,04E-10	Phenazine biosynthesis-like domain-containing protein 1	Phenazine biosynthesis protein PhzF family
Solyc01g010770.2	-1,36	1,36E-06	Hypersensitive-induced response protein 2	Spfh domain / band 7 family protein
Solyc07g005420.1	-1,36	9,62E-05	Unknown Protein	Unknown Protein
Solyc12g100030.1	-1,34	1,05E-04	Receptor-like protein 12	LRR receptor-like serine/threonine-protein kinase%2C RLP
Solyc05g050340.2	-1,34	1,01E-04	Probable wrky transcription factor 41	WRKY transcription factor 6
Solyc01g102850.1	-1,33	5,72E-08	Tmv resistance protein n-	Tir-nbs-lrr%2C resistance protein
Solyc12g006380.1	-1,33	5,64E-06	1-aminocyclopropane-1-carboxylate oxidase homolog	1-aminocyclopropane-1-carboxylate oxidase-like protein
Solyc03g026370.1	-1,32	1,34E-03	Peptidoglycan-binding domain-containing protein	Peptidoglycan-binding LysM domain-containing protein
Solyc02g063020.1	-1,31	3,39E-04	Major facilitator superfamily	Major facilitator superfamily MFS_1

			protein isoform 1	
Solyc01g006300.2	-1,31	2,11E-08	Lignin-forming anionic peroxidase-	Peroxidase
Solyc12g045020.1	-1,31	2,39E-04	Cytochrome p450 cyp736a12-	Cytochrome P450
Solyc05g007770.2	-1,31	2,98E-05	Nac transcription factor 29-like	NAC domain transcription factor
Solyc01g095170.2	-1,30	7,10E-04	Late embryogenesis abundant hydroxyproline-rich glycoprotein isoform 1	Harpin-induced protein
Solyc03g082620.2	-1,30	1,23E-06	Metal-nicotianamine transporter ysl2-like isoform x1	Oligopeptide transporter (Fragment)
Solyc04g074000.2	-1,30	4,58E-07	Probable lrr receptor-like serine threonine-protein kinase at4g08850	Receptor like kinase%2C RLK
Solyc08g016210.2	-1,30	2,81E-07	Lrr receptor-like serine threonine-protein kinase gso1	LRR receptor-like serine/threonine-protein kinase%2C RLP
Solyc02g084850.2	-1,29	6,27E-05	Unknown Protein	Unknown Protein
Solyc08g068860.2	-1,29	4,36E-09	Protein aspartic protease in guard cell 2-	Aspartic proteinase nepenthesin-1
Solyc01g080410.2	-1,29	7,74E-04	Peptide methionine sulfoxide reductase b5-	Peptide methionine sulfoxide reductase msrB
Solyc04g040130.1	-1,29	2,72E-04	Omega-6 fatty acid endoplasmic reticulum isozyme 2-	Omega-6 fatty acid desaturase
Solyc08g007460.2	-1,28	4,01E-04	Lipid transfer-like protein vas	Non-specific lipid-transfer protein
Solyc07g055710.2	-1,28	9,10E-04	Heat stress transcription factor a-4b-	Heat stress transcription factor A3
Solyc01g014840.2	-1,25	7,10E-04	Tmv resistance protein n-like isoform x1	Tir-nbs-lrr%2C resistance protein
Solyc05g050120.2	-1,25	1,17E-07	Nadp-dependent malic enzyme	Malic enzyme
Solyc04g014400.2	-1,23	1,80E-09	Lrr receptor-like serine threonine-protein kinase fls2 isoform x2	LRR receptor-like serine/threonine-protein kinase%2C RLP
Solyc05g008960.2	-1,22	5,74E-04	Probable serine threonine-protein kinase at1g18390 isoform x1	Receptor-like protein kinase
Solyc02g078380.2	-1,21	2,40E-08	Stem-specific protein tsjt1-	Aluminum-induced protein-like protein
Solyc04g009860.2	-1,20	1,39E-03	1-aminocyclopropane-1-carboxylate oxidase homolog 1-	1-aminocyclopropane-1-carboxylate oxidase-like protein
Solyc01g108790.1	-1,20	7,64E-04	3-hydroxyisobutyryl- hydrolase 1-	3-hydroxyisobutyryl-CoA hydrolase-like protein 2%2C mitochondrial
Solyc05g009500.2	-1,17	3,37E-08	Protein nrt1 ptr family	Peptide transporter
Solyc08g068870.2	-1,17	1,12E-08	Protein aspartic protease in guard cell 2-	Aspartic proteinase nepenthesin-1
Solyc02g084840.2	-1,17	2,72E-03	Cold shock protein cs66-	Dehydrin DHN1

Solyc04g006940.2	-1,16	1,44E-04	Phospholipid-transporting atpase 9	Phospholipid-transporting ATPase
Solyc07g005100.2	-1,16	3,32E-09	Class v	Chitinase-like protein
Solyc06g076560.1	-1,16	4,74E-06	Kda class i heat shock	class I heat shock protein
Solyc04g064590.1	-1,16	6,03E-04	Mitogen-activated protein kinase kinase kinase yoda-like isoform x1	Protein kinase
Solyc01g105310.2	-1,15	1,55E-04	Metacaspase-3-like isoform x2	Metacaspase
Solyc10g006750.2	-1,14	6,33E-05	Zinc finger protein constans-	CONSTANS-like zinc finger protein
Solyc09g008250.2	-1,13	1,10E-04	Transcription factor rax2-	MYB transcription factor
Solyc07g043230.2	-1,13	1,81E-05	Zinc transporter 5-	Low affinity zinc transporter
Solyc09g090080.1	-1,12	4,73E-04	Inorganic phosphate transporter 1-4-	Inorganic phosphate transporter
Solyc01g098020.2	-1,12	4,76E-06	PREDICTED: uncharacterized protein LOC101257220	Acetyltransferase GNAT family protein expressed
Solyc01g009700.1	-1,12	7,67E-05	Receptor-like protein 12	LRR receptor-like serine/threonine-protein kinase%2C RLP
Solyc01g079170.2	-1,11	6,40E-05	Galactinol synthase 1-	Galactinol synthase
Solyc12g096570.1	-1,11	7,61E-05	Argos-like protein	ARGOS
Solyc01g109500.2	-1,11	1,60E-08	Burp domain-containing protein 3-	BURP domain-containing protein
Solyc05g015490.2	-1,11	5,20E-08	Non-specific lipid transfer protein gpi-anchored 1	Non-specific lipid-transfer protein
Solyc03g078370.1	-1,11	1,96E-03	G-type lectin s-receptor-like serine threonine-protein kinase rlk1	Receptor-like protein kinase
Solyc02g085770.2	-1,10	1,13E-06	Awpm-19-like family	ABA induced plasma membrane protein PM 19
Solyc08g078040.2	-1,09	1,93E-03	Zeaxanthin chloroplastic-	Monooxygenase FAD-binding
Solyc03g120900.1	-1,09	1,48E-03	Protein transport protein sec13 homolog b	Protein transport SEC13-like protein
Solyc01g087800.2	-1,09	4,57E-04	Subtilisin-like protease	Subtilisin-like protease
Solyc08g082190.2	-1,09	1,22E-04	Keratin-associated protein 6-2-like	Unknown Protein
Solyc01g014320.2	-1,09	3,12E-05	Probable s-adenosylmethionine-dependent methyltransferase at5g38100-	S-adenosyl-L-methionine salicylic acid carboxyl methyltransferase
Solyc02g063270.2	-1,08	1,82E-06	Mate efflux family protein 5-	Multidrug and toxin extrusion protein 1
Solyc09g091660.2	-1,08	1,80E-07	Pleiotropic drug resistance protein 1-	ABC transporter G family member 40
Solyc03g119930.1	-1,08	4,92E-07	Molybdate transporter 2	Sulfate transporter like protein
Solyc12g013690.1	-1,07	7,62E-05	Zeaxanthin chloroplastic-	Monooxygenase FAD-binding protein
Solyc06g076450.2	-1,06	2,23E-03	Ras-related protein rab11a	Ras-related protein Rab-25

Solyc09g011590.2	-1,05	4,52E-06	Probable glutathione s-transferase	Glutathione S-transferase-like protein
Solyc08g065320.2	-1,05	6,94E-07	Protein reversion-to-ethylene sensitivity1	Transmembrane protein 222 (Fragment)
Solyc09g011580.2	-1,05	2,13E-07	Probable glutathione s-transferase	Glutathione S-transferase-like protein
Solyc06g007430.1	-1,05	3,73E-06	Cbl-interacting protein kinase 2-	CBL-interacting protein kinase 11
Solyc12g006530.1	-1,04	2,90E-06	Beta-amyrin synthase	Cycloartenol synthase
Solyc12g011410.1	-1,04	1,47E-04	PREDICTED: uncharacterized protein LOC107005684	Unknown Protein
Solyc04g080700.2	-1,04	1,72E-06	Bifunctional nuclease 2-like	Wound responsive protein (Fragment)
Solyc12g096710.1	-1,04	4,02E-04	Probably inactive leucine-rich repeat receptor-like protein kinase at5g48380	Receptor like kinase%2C RLK
Solyc08g005090.1	-1,04	2,72E-03	Suppressor protein srp40-	Unknown Protein
Solyc06g051360.2	-1,04	1,15E-03	Gibberellin 2-beta-dioxygenase 1	2-oxoglutarate-dependent dioxygenase
Solyc11g066860.1	-1,03	9,15E-06	PREDICTED: uncharacterized protein LOC101246792	Os02g0448600 protein (Fragment)
Solyc07g065160.2	-1,03	3,60E-04	Pirin-like protein at1g50590	Pirin
Solyc04g076990.2	-1,02	3,07E-06	Receptor-like protein kinase haiku2	Receptor like kinase%2C RLK
Solyc01g095720.2	-1,02	1,06E-05	Alpha beta-hydrolases superfamily protein	Lipase
Solyc02g079930.2	-1,01	3,17E-04	Phosphosulfolactate synthase-related protein	Phosphosulfolactate synthase
Solyc01g080220.2	-1,01	1,03E-06	Endo- -beta-d-glucanase-	Dienelactone hydrolase family protein
Solyc12g088940.1	-1,01	1,36E-03	Mitogen-activated protein kinase kinase kinase yoda-like isoform x1	Protein serine/threonine kinase
Solyc04g016230.2	-1,00	4,15E-05	Zeatin o-glucosyltransferase-	Glucosyltransferase
Solyc04g007000.1	-1,00	4,48E-04	Ap2 erf and b3 domain-containing transcription factor rav1-	Ethylene-responsive transcription factor 4
Solyc01g104690.2	-1,00	8,37E-05	PREDICTED: uncharacterized protein LOC102595557	Unknown Protein
Solyc04g081770.2	-0,99	1,38E-06	Gdsl esterase lipase exl3-	GDSL esterase/lipase At5g42170
Solyc12g098190.1	-0,99	1,24E-03	F-box protein pp2-b10-	F-box protein PP2-B1
Solyc12g094620.1	-0,98	2,35E-03	Catalase isozyme 1	Catalase
Solyc06g071820.2	-0,98	2,27E-04	Btb poz and taz domain-containing protein 1-	Speckle-type poz protein
Solyc04g077230.1	-0,97	2,55E-04	Unknown Protein	Unknown Protein
Solyc09g007980.1	-0,97	2,87E-03	Uncharacterized protein	Unknown Protein

			TCM_022188	
Solyc04g071900.2	-0,96	1,03E-04	Peroxidase 12-	Peroxidase
Solyc03g111310.2	-0,96	1,04E-05	Snf1-related protein kinase regulatory subunit gamma-1	AKIN gamma
Solyc01g008420.2	-0,96	2,94E-04	Mate efflux family protein 1-like isoform x1	Mate efflux family protein
Solyc11g010700.1	-0,95	7,69E-05	U-box domain-containing protein 50	Receptor-like protein kinase
Solyc02g085940.2	-0,95	9,63E-06	Ribulose bisphosphate carboxylase	Unknown Protein
Solyc01g086870.2	-0,95	1,51E-04	Transcription factor bhlh130-	BHLH transcription factor
Solyc04g080640.1	-0,95	1,69E-03	PREDICTED: uncharacterized protein LOC101245645	Genomic DNA chromosome 5 TAC clone K1F13
Solyc02g093750.2	-0,95	9,67E-04	Upf0392 protein rcom_0530710-	Ring zinc finger protein (Fragment)
Solyc01g106400.2	-0,95	1,73E-05	Peptide methionine sulfoxide reductase b5-	Peptide methionine sulfoxide reductase msrB
Solyc02g071020.2	-0,94	3,23E-05	Chlorophyll a-b binding protein chloroplastic-	Unknown Protein
Solyc04g057940.2	-0,94	7,66E-05	E3 ubiquitin-protein ligase lin-1 isoform x1	U-box domain-containing protein
Solyc10g076550.1	-0,94	2,55E-04	Wall-associated receptor kinase 2-	Receptor-like protein kinase At3g21340
Solyc02g086880.2	-0,94	2,21E-05	Formate mitochondrial	Formate dehydrogenase
Solyc01g106000.2	-0,94	1,70E-05	Nicotinamidase 1 isoform 1	Isochorismatase hydrolase
Solyc05g006420.2	-0,94	1,74E-06	Two-component response regulator arr5	Two-component response regulator ARR3
Solyc10g012080.2	-0,94	8,35E-04	Pollen-specific leucine-rich repeat extensin-like protein 3 isoform x1	MRNA clone RAFL21-79-C21
Solyc01g094790.2	-0,93	5,66E-04	Bifunctional l-3-cyanoalanine synthase cysteine synthase mitochondrial	Cysteine synthase
Solyc07g006480.2	-0,93	3,01E-04	Probably inactive leucine-rich repeat receptor-like protein kinase at5g48380	LRR receptor-like serine/threonine-protein kinase FEI 1
Solyc04g079220.1	-0,93	4,23E-04	Patatin-like protein 2	Patatin-like protein 1
Solyc07g055470.2	-0,93	4,11E-05	Cytochrome p450 cyp72a219-	Cytochrome P450
Solyc02g063450.2	-0,93	4,63E-05	PREDICTED: uncharacterized protein LOC101249886	Hypothetical YFW family protein 5
Solyc11g028080.1	-0,92	4,11E-04	PREDICTED: uncharacterized protein LOC101249425	Unknown Protein
Solyc04g079230.2	-0,92	6,57E-06	Patatin-like protein 2	Patatin-like protein 1
Solyc05g013810.2	-0,92	8,25E-05	Cellulase protein	Glycosyl hydrolase family 5 protein/cellulase

Solyc12g099190.1	-0,92	1,12E-03	Invertase inhibitor	Invertase inhibitor
Solyc12g088250.1	-0,90	4,45E-05	Serine carboxypeptidase-	Serine carboxypeptidase 1
Solyc09g098030.2	-0,90	2,48E-06	Geraniol 8-hydroxylase-	Cytochrome P450
Solyc09g011660.2	-0,89	7,61E-04	Universal stress protein a-like protein	Universal stress protein 1
Solyc04g008330.1	-0,89	1,81E-05	Zeatin o-glucosyltransferase-	Glucosyltransferase
Solyc02g077590.1	-0,89	1,00E-05	Homeobox-leucine zipper protein athb-52-	Homeobox-leucine zipper-like protein
Solyc03g097930.2	-0,89	1,26E-03	Potassium channel skor-	Unknown Protein
Solyc09g007270.2	-0,88	2,71E-05	L-ascorbate peroxidase cytosolic	Ascorbate peroxidase
Solyc05g015800.2	-0,88	2,09E-05	Methanol o-anthraniloyltransferase-	Acetyl coenzyme A cis-3-hexen-1-ol acetyl transferase
Solyc11g007200.1	-0,88	7,15E-06	Copper transport protein cch-	Copper chaperone
Solyc04g011670.2	-0,88	2,18E-04	Tgacg-sequence-specific dna-binding protein tga-1a isoform x2	BZIP transcription factor
Solyc02g082060.1	-0,88	5,26E-05	Desi-like protein at4g17486	PPPDE peptidase domain-containing protein 1
Solyc07g054760.1	-0,87	2,83E-03	Wound induced protein	Wound induced protein
Solyc11g013150.1	-0,87	3,61E-04	Nodulation-signaling pathway 2 protein	GRAS family transcription factor
Solyc01g108300.2	-0,87	2,31E-04	Two-component response regulator-like aprr2	Myb family transcription factor
Solyc04g079210.2	-0,86	1,53E-05	Patatin-like protein 2	Patatin-like protein 1
Solyc07g044980.2	-0,86	2,20E-05	Regulatory protein npr3-like isoform x1	NPR1-1 protein (Fragment)
Solyc12g006450.1	-0,85	1,28E-05	Gamma aminobutyrate transaminase chloroplastic isoform x2	Aminotransferase-like protein
Solyc07g063750.2	-0,85	9,38E-05	G-type lectin s-receptor-like serine threonine-protein kinase at4g27290	Serine/threonine-protein kinase receptor
Solyc09g011560.2	-0,85	4,38E-04	Probable glutathione s-transferase	Glutathione S-transferase-like protein
Solyc09g090110.2	-0,85	1,38E-05	Actin-depolymerizing factor	Actin depolymerizing factor 6
Solyc09g097780.2	-0,84	6,78E-05	Glycine-rich protein precursor	Glycine-rich protein
Solyc04g078200.2	-0,84	1,47E-04	Snakin-1	Gibberellin-regulated family protein
Solyc10g049970.1	-0,84	1,64E-05	Kynurenine formamidase-	Kynurenine formamidase
Solyc03g025720.2	-0,83	5,81E-04	4-coumarate-- ligase-	Long-chain-fatty-acid--CoA ligase
Solyc09g072590.2	-0,83	8,96E-05	Actin-depolymerizing factor	Actin-depolymerizing factor 6
Solyc09g089860.2	-0,83	2,00E-03	Wat1-related protein	Nodulin-like protein

			at5g07050-	
Solyc12g099600.1	-0,83	7,85E-05	Probable protein phosphatase 2c 40	Protein phosphatase 2C containing protein
Solyc12g096030.1	-0,82	1,64E-03	Solute carrier family 25 member 44-	Mitochondrial carrier-like protein
Solyc04g005160.1	-0,82	3,07E-05	6-phosphogluconate decarboxylating 3	6-phosphogluconate dehydrogenase decarboxylating
Solyc11g064920.1	-0,82	5,97E-05	Dihydropyrimidinase	Dihydropyrimidinase
Solyc05g010450.1	-0,82	2,95E-04	Micronuclear linker histone poly	Unknown Protein
Solyc04g016430.2	-0,82	3,52E-04	Cytokinin dehydrogenase 1-	Cytokinin oxidase/dehydrogenase 1
Solyc01g090680.2	-0,81	2,31E-03	PREDICTED: uncharacterized protein LOC101265167	Genomic DNA chromosome 5 TAC clone K11J9
Solyc08g067540.1	-0,80	1,80E-04	Non-specific lipid-transfer protein 1-	Non-specific lipid-transfer protein
Solyc04g014530.1	-0,80	1,66E-03	Ethylene-responsive transcription factor 1b-	Ethylene responsive transcription factor 1a
Solyc10g083380.1	-0,80	2,42E-03	Bzip transcription factor family protein	Unknown Protein
Solyc01g087620.2	-0,80	7,35E-05	Ubiquitin-like protein 5	Unknown Protein
Solyc09g090430.2	-0,79	2,16E-04	Cyanate hydratase	Cyanate hydratase
Solyc10g083860.1	-0,79	1,06E-04	Udp-glycosyltransferase 73c6-	UDP-glucosyltransferase family 1 protein
Solyc05g052030.1	-0,79	2,25E-03	Ethylene-responsive transcription factor erf106-	Ethylene responsive transcription factor 1a
Solyc01g099840.2	-0,79	8,37E-04	Auxin-repressed kda	Auxin-repressed protein
Solyc03g082690.2	-0,79	7,55E-04	U-box domain-containing protein 44-	U-box domain-containing protein
Solyc08g068150.2	-0,79	5,14E-04	Dehydration-responsive protein rd22	BURP domain-containing protein
Solyc00g289230.1	-0,79	2,51E-03	Unknown Protein	Receptor protein kinase
Solyc01g009860.2	-0,78	9,71E-05	Nac transcription factor 29-	NAC domain transcription factor
Solyc11g011920.1	-0,78	1,29E-03	Glutamate decarboxylase	Glutamate decarboxylase
Solyc12g045030.1	-0,78	1,26E-03	Probable l-xylulose reductase	Short-chain dehydrogenase/reductase family protein
Solyc01g007920.2	-0,78	5,45E-04	Isochorismatase hydrolase family protein	Isochorismatase family protein
Solyc09g090070.1	-0,77	6,79E-05	Phosphate transporter	Inorganic phosphate transporter
Solyc02g082080.1	-0,77	8,61E-05	Copper transporter 5	High affinity copper uptake protein
Solyc06g060250.2	-0,76	1,63E-04	Aldehyde dehydrogenase family 3 member h1	Aldehyde dehydrogenase family protein expressed
Solyc02g081850.2	-0,76	6,84E-05	Cationic amino acid transporter 5	Amino acid transporter
Solyc05g055310.2	-0,76	9,21E-05	Copper chaperone	Copper chaperone

Solyc08g062210.2	-0,76	2,50E-04	Nuclear transcription factor y subunit a-3-	Nuclear transcription factor Y subunit A-3
Solyc01g094910.2	-0,76	6,57E-05	Ferric reduction oxidase 2-	Ferric reductase oxidase
Solyc08g067960.2	-0,75	9,96E-04	Ring finger and chy zinc finger domain-containing protein 1	CHY zinc finger family protein expressed
Solyc11g065820.1	-0,75	1,34E-03	Mate efflux family protein 1	Mate efflux family protein
Solyc11g011880.1	-0,75	1,09E-03	Cysteine-rich receptor-like protein kinase 2	RLK%2C Receptor like protein%2C putative resistance protein with an antifungal domain
Solyc06g082590.1	-0,74	1,30E-03	Pathogenesis-related genes transcriptional activator pti6-	Ethylene responsive transcription factor 1b
Solyc05g008110.2	-0,74	3,80E-04	PREDICTED: mulatexin	Unknown Protein
Solyc10g007050.2	-0,74	2,06E-04	Probable bifunctional methylthioribulose-1-phosphate dehydratase enolase-phosphatase e1 1	Enolase-phosphatase E-1
Solyc06g063090.2	-0,74	2,17E-04	Alanine aminotransferase 2-	Alanine aminotransferase
Solyc10g054670.1	-0,73	2,61E-03	Unknown Protein	Unknown Protein
Solyc04g017690.2	-0,73	6,40E-04	Protein early responsive to dehydration 15-	Early response to dehydration 15-like protein (Fragment)
Solyc02g091100.2	-0,73	2,16E-04	2-hydroxyacyl- lyase	Oxalyl-CoA decarboxylase
Solyc03g118970.2	-0,73	1,52E-04	Mate efflux family protein 5-	Multidrug resistance protein mdtK
Solyc03g019880.2	-0,73	1,58E-04	Upf0426 protein chloroplastic	UPF0426 protein At1g28150%2C chloroplastic
Solyc01g090900.2	-0,72	4,14E-04	Cytochrome p450	Unknown Protein
Solyc08g007790.2	-0,71	6,22E-04	Hydroxymethylglutaryl-synthase-like	Hydroxymethylglutaryl-CoA synthase
Solyc03g111800.2	-0,71	7,29E-04	Leucine-rich repeat receptor-like serine threonine tyrosine-protein kinase sobir1	Receptor like kinase%2C RLK
Solyc03g116110.2	-0,70	5,73E-04	Alpha beta hydrolase family protein	Alpha/beta hydrolase fold protein
Solyc10g078600.1	-0,70	4,88E-04	Mannose-binding lectin superfamily isoform 1	Myrosinase-binding protein (Fragment)
Solyc11g069290.1	-0,69	2,62E-04	Pyridoxal biosynthesis protein pdx2	Glutamine amidotransferase subunit pdxT
Solyc01g009430.2	-0,69	8,33E-04	PREDICTED: uncharacterized protein At4g22758-	Os02g0448600 protein (Fragment)
Solyc01g104720.2	-0,69	3,41E-04	Nodulin 21 -like transporter family isoform 1	Unknown Protein
Solyc01g105970.2	-0,69	1,04E-03	Magnesium-dependent phosphatase 1-	Magnesium-dependent phosphatase-1 family protein expressed
Solyc01g100660.2	-0,69	7,19E-04	Transcription factor bhlh147-	Transcription factor
Solyc01g086810.2	-0,68	2,52E-04	Disease resistance protein rpm1-	Cc-nbs-lrr%2C resistance protein

Solyc06g030490.2	-0,68	1,79E-03	Serine threonine-protein phosphatase pp1 isozyme 4	Serine/threonine-protein phosphatase
Solyc07g007270.2	-0,68	1,22E-03	PREDICTED: uncharacterized protein LOC101253390	Unknown Protein
Solyc01g112100.2	-0,68	6,30E-04	Probable flavin-containing monooxygenase 1	Dimethylaniline monooxygenase 5
Solyc02g083970.1	-0,68	5,11E-04	PREDICTED: uncharacterized protein LOC101258023	Chromosome 18 contig 1 DNA sequence
Solyc03g121270.2	-0,68	4,34E-04	Iaa-amino acid hydrolase ilr1-	IAA-amino acid hydrolase
Solyc02g087060.2	-0,67	9,64E-04	Wat1-related protein at3g28050-	Nodulin MtN21 family protein
Solyc03g031920.2	-0,67	1,01E-03	Probable metal-nicotianamine transporter ysl7	Yellow stripe-like protein 2.1 (Fragment)
Solyc07g043310.2	-0,67	4,93E-04	Gamma aminobutyrate transaminase mitochondrial	Aminotransferase
Solyc09g082120.2	-0,67	1,31E-03	Lactoylglutathione lyase	Glyoxalase/bleomycin resistance protein/dioxygenase
Solyc04g080810.2	-0,67	1,14E-03	Probable ubiquitin-conjugating enzyme e2 18	Ubiquitin-conjugating enzyme E2 W
Solyc01g104060.2	-0,66	1,02E-03	Mitochondrial isoform x1	Aminomethyltransferase
Solyc09g090980.2	-0,66	1,33E-03	Pathogenesis-related protein sth-2-	Major allergen Mal d 1
Solyc01g102660.2	-0,66	7,97E-04	Glutathione s-transferase zeta class-	Maleylacetoacetate isomerase / glutathione S-transferase
Solyc09g082730.2	-0,66	5,29E-04	Perakine reductase-	Aldo/keto reductase family protein
Solyc09g083020.1	-0,66	8,25E-04	Inactive protein restricted tev movement 1-	Myrosinase-binding protein-like protein
Solyc09g082060.2	-0,66	2,24E-03	Cysteine synthase	Cysteine synthase
Solyc05g009780.2	-0,66	1,16E-03	Methionine aminopeptidase chloroplastic	Methionine aminopeptidase
Solyc02g084740.2	-0,66	1,34E-03	3-epi-6-deoxocathasterone 23-monooxygenase	Cytochrome P450
Solyc03g123610.2	-0,65	5,49E-04	Alanine aminotransferase 2	Alanine aminotransferase
Solyc01g105420.2	-0,65	1,37E-03	Phospho-2-dehydro-3-deoxyheptonate aldolase chloroplastic-	Phospho-2-dehydro-3-deoxyheptonate aldolase 2
Solyc12g042770.1	-0,65	1,56E-03	Post-illumination chlorophyll fluorescence increase isoform 1	Chloroplast post-illumination chlorophyll fluorescence increase protein
Solyc05g006850.2	-0,65	6,94E-04	Thioredoxin h2-	Thioredoxin H
Solyc02g089930.2	-0,65	1,39E-03	Protein da1-related 1-	Homeobox protein LIM-3 (Fragment)
Solyc01g009020.2	-0,65	1,32E-03	Cysteine proteinase inhibitor	Cysteine proteinase inhibitor
Solyc01g087640.2	-0,65	5,22E-04	Cinnamoyl- reductase 1-	Cinnamoyl CoA reductase-like protein
Solyc09g091840.2	-0,64	1,14E-03	Glutathione chloroplastic	Glutathione-disulfide reductase
Solyc04g080010.2	-0,64	1,62E-03	Hydroquinone	UDP-glucosyltransferase

			glucosyltransferase-	
Solyc02g068240.2	-0,64	2,45E-03	Diacylglycerol o-acyltransferase 2	Diacylglycerol acyltransferase family
Solyc07g063010.2	-0,63	1,74E-03	Probable 3-hydroxyacyl-dehydrogenase	Fatty acid oxidation complex subunit alpha
Solyc07g045190.1	-0,63	2,22E-03	Probable e3 ubiquitin-protein ligase xerico	RING-H2 finger protein
Solyc07g042550.2	-0,63	1,97E-03	Sucrose synthase	Sucrose synthase
Solyc02g085310.2	-0,63	2,74E-03	Unknown Protein	Unknown Protein
Solyc07g063570.2	-0,62	1,20E-03	Cytochrome c-type biogenesis ccda-like chloroplastic protein	Cytochrome c biogenesis protein family
Solyc04g076040.2	-0,62	2,08E-03	D2 4-type cyclin	Cyclin d2
Solyc01g100920.2	-0,62	1,60E-03	Wat1-related protein at1g09380-	Nodulin-like protein
Solyc08g075860.2	-0,61	2,74E-03	PREDICTED: uncharacterized protein LOC101259778	Os06g0115800 protein (Fragment)
Solyc03g114950.2	-0,61	1,68E-03	Abc transporter b family member 25	Lipid a export ATP-binding/permease protein msba
Solyc04g074750.2	-0,61	1,64E-03	28 kda chloroplastic	Polyadenylate-binding protein 1-A
Solyc08g077780.2	-0,61	2,47E-03	Serine threonine-protein kinase sapk3-	Serine/threonine protein kinase
Solyc09g065300.2	-0,61	2,54E-03	PREDICTED: uncharacterized protein LOC107031422 isoform X1	Uncharacterized membrane protein
Solyc01g099100.2	-0,61	2,16E-03	Long chain acyl- synthetase peroxisomal-	Long-chain-fatty-acid coa ligase
Solyc02g085640.2	-0,61	1,30E-03	Probable xaa-pro aminopeptidase p	Xaa-Pro aminopeptidase 1
Solyc06g060790.1	-0,61	2,50E-03	3-isopropylmalate dehydratase small subunit 3-	3-isopropylmalate dehydratase small subunit
Solyc10g006270.2	-0,60	1,81E-03	Autophagy-related protein 8c	Autophagy-related protein 8
Solyc04g011520.2	-0,60	2,78E-03	Protein kinase chloroplastic	Serine/threonine kinase-like protein ABC1063
Solyc10g045240.1	-0,60	1,58E-03	Vicianin hydrolase-	Beta-glucosidase D4
Solyc11g007590.1	-0,59	2,41E-03	Otu domain-containing protein at3g57810-	OTU domain-containing protein 4
Solyc08g029160.1	-0,59	1,63E-03	Probable steroid-binding protein 3	Membrane-associated progesterone receptor component 2
Solyc09g059040.2	-0,59	2,09E-03	Quinone-oxidoreductase chloroplastic	Alcohol dehydrogenase zinc-containing
Solyc12g100200.1	-0,59	2,47E-03	Selenoprotein o-	Protein YdiU
Solyc04g005650.1	-0,59	2,26E-03	Peroxisomal nicotinamide adenine dinucleotide carrier-	Mitochondrial carrier family
Solyc09g005620.2	-0,59	2,34E-03	Monothiol glutaredoxin-chloroplastic	Glutaredoxin

Solyc12g096120.1	-0,58	1,62E-03	Ubiquitin-fold modifier 1	Ubiquitin-fold modifier 1
Solyc06g082010.2	-0,58	2,68E-03	Zinc finger ccch domain-containing protein 66-like isoform x2	Zinc finger CCCH domain-containing protein 66
Solyc10g084400.1	-0,58	2,63E-03	Glutathione s-transferase l3-like isoform x1	Glutathione S-transferase
Solyc10g054820.1	-0,57	2,46E-03	X intrinsic protein	Aquaporin
Solyc06g060260.2	-0,57	2,41E-03	Probable l-ascorbate peroxidase chloroplastic isoform x1	Stromal ascorbate peroxidase 7
Solyc02g063490.2	-0,57	2,88E-03	Malate glyoxysomal	Malate dehydrogenase
Solyc10g052580.1	-9,82	5,51E-08	Auxin-induced protein 15a-	Auxin-induced SAUR-like protein
Solyc06g035940.2	-9,14	2,60E-08	Homeobox-leucine zipper protein anthocyaninless 2-like isoform x2	Homeobox-leucine zipper protein PROTODERMAL FACTOR 2
Solyc10g052570.1	-6,96	3,97E-05	Auxin-induced protein 6b-	Auxin-responsive protein
Solyc09g089490.2	-6,36	7,82E-06	Proteinase inhibitor i-b-	Proteinase inhibitor I
Solyc02g083480.2	-5,30	5,79E-07	Peroxidase 64-	Peroxidase
Solyc12g006730.1	-5,02	2,91E-05	Unknown Protein	Unknown Protein
Solyc12g006750.1	-4,79	9,15E-05	Unknown Protein	Unknown Protein
Solyc00g020540.1	-4,71	1,87E-04	Unknown Protein	Aminotransferase-like protein
Solyc05g051720.1	-4,57	5,01E-06	Monothiol glutaredoxin-s1-	Glutaredoxin
Solyc07g044900.1	-4,24	9,24E-04	Unknown Protein	Unknown Protein
Solyc07g052070.1	-4,01	5,67E-04	Cytochrome p450 cyp72a219-	Cytochrome P450
Solyc02g067750.2	-3,85	9,09E-05	Carbonic chloroplastic-	Carbonic anhydrase
Solyc04g071780.2	-3,42	4,46E-09	Cytochrome p450 71a1-	Cytochrome P450
Solyc09g097960.2	-3,34	3,91E-05	Auxin-induced protein pcnt115-	Aldo/keto reductase family protein
Solyc09g082810.2	-3,28	3,53E-26	S14981extensin class i (clone w1-8 l) - tomato	Unknown Protein
Solyc05g051730.1	-3,24	1,03E-04	Monothiol glutaredoxin-s1-	Glutaredoxin
Solyc05g052400.2	-3,16	3,00E-04	Laccase-12-	Laccase
Solyc02g071560.2	-3,08	2,23E-07	Subtilisin-like protease	Subtilisin-like protease
Solyc05g012850.2	-2,91	4,69E-05	PREDICTED: uncharacterized protein LOC101256182	Unknown Protein
Solyc12g057020.1	-2,89	6,00E-05	Probable carbohydrate esterase at4g34215	Acetyl xylan esterase A
Solyc02g071470.2	-2,87	8,03E-08	Protein srg1-	1-aminocyclopropane-1-carboxylate oxidase 1
Solyc08g080670.1	-2,74	9,54E-04	Osmotin-like protein	Osmotin-like protein (Fragment)
Solyc07g052140.2	-2,72	3,09E-08	(-)-Germacrene d synthase-	(-)-germacrene D synthase

Solyc12g088240.1	-2,62	1,63E-03	Probable xyloglucan glycosyltransferase 12	Cellulose synthase-like C1-1 glycosyltransferase family 2 protein
Solyc02g032660.2	-2,60	6,09E-10	Protein transparent testa 12-like	MATE efflux family protein expressed
Solyc01g103920.2	-2,52	8,06E-07	Ferredoxin	Ferredoxin I
Solyc07g044910.1	-2,49	1,79E-03	Unknown Protein	Unknown Protein
Solyc09g059220.1	-2,44	2,02E-03	PREDICTED: uncharacterized protein LOC101247252	Unknown Protein
Solyc08g080620.1	-2,38	6,10E-06	Osmotin-like protein	Osmotin-like protein (Fragment)
Solyc12g042010.1	-2,37	2,77E-05	Transcription factor ibh1-	Unknown Protein
Solyc11g069700.1	-2,35	6,03E-12	Elongation factor 1-alpha-	Elongation factor 1-alpha
Solyc07g064650.1	-2,31	1,46E-03	Phospholipase d c-	Arabidopsis thaliana genomic DNA chromosome 5 P1 clone MOK16
Solyc04g072700.2	-2,30	1,78E-08	Heavy metal-associated isoprenylated plant protein 26-	Metal ion binding protein
Solyc01g105810.2	-2,27	1,36E-03	Guanosine nucleotide diphosphate dissociation inhibitor at5g09550	Rab-GDP dissociation inhibitor
Solyc11g066270.1	-2,24	1,23E-04	Probable xyloglucan endotransglucosylase hydrolase protein 31	Xyloglucan endotransglucosylase/hydrolase 9
Solyc09g008760.1	-2,24	1,12E-06	Serine arginine repetitive matrix protein 2-	Unknown Protein
Solyc03g098760.1	-2,17	1,28E-03	Kunitz-type inhibitor b	Kunitz-type protease inhibitor-like protein
Solyc12g013830.1	-2,16	1,38E-04	Unknown Protein	Unknown Protein
Solyc02g061770.2	-2,14	7,08E-04	Basic endochitinase-	Endochitinase (Chitinase)
Solyc07g008520.2	-2,12	1,27E-05	Protein nrt1 ptr family -	Peptide transporter
Solyc01g081170.1	-2,07	2,69E-04	Beta-glucosidase 11-	Beta-glucosidase
Solyc11g005480.1	-2,00	2,23E-03	Citrate-binding	Citrate binding protein
Solyc10g055820.1	-1,98	3,85E-05	Endochitinase 3-	Chitinase
Solyc01g081160.2	-1,97	9,29E-04	Beta-glucosidase 11-like isoform x2	Beta-glucosidase
Solyc04g050620.2	-1,97	3,37E-07	Cytochrome p450 cyp736a12-	Cytochrome P450
Solyc02g079710.2	-1,93	4,36E-04	G-type lectin s-receptor-like serine threonine-protein kinase at4g27290	Serine/threonine kinase receptor
Solyc09g010160.1	-1,92	4,46E-06	Nac domain-containing protein 90-	NAC domain protein IPR003441
Solyc03g020010.1	-1,91	1,56E-03	Miraculin	Kunitz-type trypsin inhibitor alpha chain
Solyc07g008210.2	-1,91	5,78E-09	Tetratricopeptide repeat-superfamily	TPR domain protein
Solyc03g118850.2	-1,81	5,06E-04	PREDICTED: uncharacterized protein LOC101245242	Hydrolase alpha/beta fold family

Solyc02g068170.1	-1,81	6,04E-05	PREDICTED: uncharacterized protein LOC105632422	Unknown Protein
Solyc10g085880.1	-1,81	3,93E-06	Udp-glycosyltransferase 73c3-	UDP-glucosyltransferase family 1 protein
Solyc02g072550.1	-1,80	1,39E-03	Transcription factor hbp-1b -	DOG1 alpha splice variant (Fragment)
Solyc07g055560.2	-1,80	4,52E-07	Cytochrome p450 cyp72a219-	G-type lectin S-receptor-like serine/threonine-protein kinase At2g19130
Solyc07g062480.1	-1,79	3,96E-05	Epidermis-specific secreted glycoprotein ep1-	S-locus glycoprotein (Fragment)
Solyc01g100490.2	-1,79	8,74E-07	Nicotianamine synthase	Nicotianamine synthase
Solyc07g055840.2	-1,78	4,66E-07	Citrate glyoxysomal-	Citrate synthase
Solyc06g050790.2	-1,75	2,39E-05	Sodium-coupled neutral amino acid transporter 7	Amino acid transporter
Solyc08g079900.1	-1,74	1,99E-07	Subtilisin-like protease	Subtilisin-like protease
Solyc03g121010.2	-1,74	7,10E-04	Unknown Protein	Unknown Protein
Solyc04g005810.2	-1,74	9,91E-05	Thioredoxin h2-	Thioredoxin H
Solyc01g106820.2	-1,72	9,42E-07	Probable zinc metallopeptidase chloroplastic	Peptidase M50 family
Solyc04g079470.2	-1,72	2,38E-03	Serpin-zx-	Serpin (Serine protease inhibitor)
Solyc08g007430.1	-1,70	2,43E-03	Protein nrt1 ptr family -	Nitrate transporter
Solyc11g044440.1	-1,69	6,71E-05	Serine threonine-protein phosphatase 7 long form homolog	Serine/threonine-protein phosphatase 7 long form homolog
Solyc02g036480.1	-1,69	1,79E-03	Protein yls9-	Harpin-induced protein-like (Fragment)
Solyc01g010480.2	-1,67	7,29E-11	Protein twin lov 1	Potassium voltage-gated channel subfamily H member 8
Solyc01g094140.2	-1,64	1,03E-03	Cytochrome p450 704c1-	Cytochrome P450
Solyc00g282510.1	-1,62	5,16E-05	Unknown Protein	Phenylalanine ammonia-lyase
Solyc10g080230.1	-1,61	1,72E-05	Gata zinc finger domain-containing protein 8-	DNA binding protein-like
Solyc01g096320.2	-1,59	1,66E-05	Homeobox-leucine zipper protein athb-12-	Homeobox leucine zipper protein
Solyc06g054570.1	-1,59	7,18E-04	Monothiol glutaredoxin-s4-	Glutaredoxin family protein
Solyc08g077370.2	-1,58	1,03E-03	Probable purine permease 11	Purine permease family protein
Solyc02g089490.2	-1,57	1,82E-03	PREDICTED: uncharacterized protein LOC102592499 isoform X1	Unknown Protein
Solyc07g062500.2	-1,54	9,69E-06	Cytochrome p450 cyp72a219-	Cytochrome P450
Solyc10g080240.1	-1,54	9,37E-04	Gata zinc finger domain-containing protein 8-	Remorin family protein
Solyc07g042520.2	-1,54	6,64E-06	Sucrose synthase	Sucrose synthase 4
Solyc02g063410.2	-1,53	1,56E-03	PREDICTED: uncharacterized protein At5g65660-	Hydroxyproline-rich glycoprotein

Solyc07g056200.2	-1,52	6,05E-05	Metal ion binding	NBS-LRR class disease resistance protein
Solyc06g084820.1	-1,52	7,12E-07	Geraniol 8-hydroxylase-	cytochrome P450
Solyc11g045460.1	-1,50	1,70E-03	Probable carboxylesterase 15	CXE carboxylesterase
Solyc07g064600.2	-1,48	2,01E-03	Ribonuclease uk114-	Endoribonuclease L-PSP family protein
Solyc11g066590.1	-1,48	6,22E-09	Lysosomal pro-x carboxypeptidase-	Lysosomal Pro-X carboxypeptidase
Solyc02g070020.1	-1,47	6,56E-05	Udp-glycosyltransferase 91c1	UDP-glucosyltransferase
Solyc07g017610.2	-1,45	1,45E-08	Alpha-aminoadipic semialdehyde synthase	Saccharopine dehydrogenase
Solyc06g050800.2	-1,42	3,63E-06	Probable sodium-coupled neutral amino acid transporter 6	Amino acid transporter
Solyc04g009850.2	-1,42	6,00E-05	1-aminocyclopropane-1-carboxylate oxidase homolog 1-	1-aminocyclopropane-1-carboxylate oxidase-like protein
Solyc02g079870.2	-1,42	4,96E-08	PREDICTED: uncharacterized protein LOC101267080	Unknown Protein
Solyc04g005610.2	-1,40	3,59E-04	Nac transcription factor 29-	NAC domain transcription factor
Solyc03g083420.2	-1,40	1,09E-03	Probable plastid-lipid-associated protein chloroplastic isoform x1	OBP3-responsive gene 1
Solyc04g072380.2	-1,40	6,45E-04	Vacuolar membrane-associated iml1	Phosphatidylinositol 3%2C4%2C5-trisphosphate-dependent Rac exchanger 2 protein
Solyc06g076330.2	-1,38	1,06E-03	Laccase 2	Laccase
Solyc06g069430.2	-1,37	3,39E-05	Agamous-like mads-box protein agl8 homolog	MADS box transcription factor
Solyc04g053110.1	-1,37	1,05E-03	Monothiol glutaredoxin-s6-like	Glutaredoxin
Solyc01g005230.2	-1,36	8,82E-04	Probable s-adenosylmethionine-dependent methyltransferase at5g38100-	S-adenosyl-L-methionine salicylic acid carboxyl methyltransferase
Solyc07g008310.2	-1,35	6,03E-08	Choline chloroplastic-	Rieske (2Fe-2S) domain protein
Solyc05g054750.2	-1,32	3,00E-06	PREDICTED: uncharacterized protein LOC101266225 isoform X1	Plant-specific domain TIGR01589 family protein
Solyc02g063510.1	-1,32	1,99E-03	PREDICTED: uncharacterized protein LOC101267773	Unknown Protein
Solyc09g083200.2	-1,32	4,62E-05	Protein lyk5-	Nod factor receptor protein (Fragment)
Solyc07g008240.2	-1,30	1,47E-03	Non-symbiotic hemoglobin 1	Non-symbiotic hemoglobin protein
Solyc05g050130.2	-1,29	4,60E-07	Acidic endochitinase	Acidic chitinase
Solyc09g075210.2	-1,29	3,35E-04	Late embryogenesis abundant protein lea5-	Late embryogenesis abundant protein 5
Solyc04g007800.2	-1,29	1,58E-05	Probable adp-ribosylation factor gtpase-activating protein agd11	C2 domain-containing protein
Solyc03g078150.2	-1,29	4,63E-04	Vacuolar amino acid transporter 1 isoform x6	Amino acid transporter family protein

Solyc03g098240.2	-1,29	8,49E-06	Glutamate decarboxylase-	Glutamate decarboxylase
Solyc01g107820.2	-1,27	6,71E-07	Scopoletin glucosyltransferase-	UDP-glucosyltransferase family 1 protein
Solyc01g106620.2	-1,26	5,64E-05	Basic form of pathogenesis-related protein 1-	Pathogenesis-related protein 1a
Solyc04g007990.1	-1,26	6,30E-05	PREDICTED: uncharacterized protein LOC104646728	Unknown Protein
Solyc04g072760.2	-1,25	1,23E-03	Sulfate transporter -	High affinity sulfate transporter 2
Solyc05g051850.2	-1,24	8,09E-04	Inositol-3-phosphate synthase	Inositol-3-phosphate synthase
Solyc11g011440.1	-1,24	1,06E-05	Aspartic proteinase pcs1-	Aspartic proteinase nepenthesin-1
Solyc01g081270.2	-1,23	7,82E-04	Glutathione transferase gst 23-	Glutathione S-transferase
Solyc07g041900.2	-1,23	6,07E-04	Cysteine proteinase 3-	Cathepsin L-like cysteine proteinase
Solyc12g013620.1	-1,20	6,68E-04	Nac domain-containing protein 72-	NAC domain protein IPR003441
Solyc06g076470.2	-1,19	3,15E-05	PREDICTED: uncharacterized protein LOC101267414 isoform X1	Unknown Protein
Solyc06g071070.1	-1,19	3,45E-04	Short-chain type dehydrogenase reductase-	Short-chain dehydrogenase/reductase family protein
Solyc03g044790.2	-1,18	1,66E-03	Salicylic acid-binding protein 2-	Alpha-hydroxynitrile lyase
Solyc08g076050.2	-1,18	5,83E-05	G-type lectin s-receptor- serine threonine-protein kinase at1g67520	ARK3 product/receptor-like serine/threonine protein kinase ARK3
Solyc07g007150.1	-1,17	6,73E-04	PREDICTED: uncharacterized protein LOC104648246	Unknown Protein
Solyc01g081310.2	-1,17	8,68E-05	Glutathione transferase gst 23-	Glutathione-S-transferase
Solyc04g079480.2	-1,17	1,34E-03	Serpin-zx-	Serpin (Serine protease inhibitor)
Solyc06g076520.1	-1,16	2,41E-05	Kda class i heat shock	class I heat shock protein
Solyc03g113270.2	-1,14	3,67E-05	Homeobox-leucine zipper protein hat5-	Homeobox-leucine zipper-like protein
Solyc10g085140.1	-1,14	8,09E-06	Dehydrodolichyl diphosphate synthase 2-	Undecaprenyl pyrophosphate synthase
Solyc02g072470.2	-1,14	6,22E-04	Probable lrr receptor-like serine threonine-protein kinase at3g47570	Receptor like kinase%2C RLK
Solyc08g082120.2	-1,13	9,73E-05	Methanol inducible protein	Methanol inducible protein
Solyc01g091870.2	-1,12	5,51E-04	Spx domain-containing membrane protein at4g22990-	Major facilitator superfamily domain-containing protein 8
Solyc07g008020.2	-1,12	1,99E-06	Auxin-responsive protein iaa29-	Auxin response factor 16
Solyc01g095320.2	-1,12	2,16E-03	Bag family molecular chaperone regulator 6	BCL-2-associated athanogene 6
Solyc01g108540.2	-1,12	1,51E-03	2-hydroxyisoflavanone dehydratase-	Acetyl esterase

Solyc03g031990.2	-1,12	1,81E-03	Uncharacterized transporter ybr287w-	Auxin efflux carrier family protein
Solyc01g008510.2	-1,11	2,63E-03	Photosystem ii 5 kda chloroplastic-	Photosystem II 5 kDa protein%2C chloroplastic
Solyc08g067310.1	-1,10	1,03E-03	Cbl-interacting serine threonine-protein kinase 5-	CBL-interacting protein kinase 6
Solyc01g096340.2	-1,10	1,51E-05	Auxin-induced protein 15a-	Auxin-induced SAUR-like protein
Solyc03g123710.2	-1,10	4,08E-04	Hypothetical protein MIMGU_mgv1a017182mg	Unknown Protein
Solyc01g005410.2	-1,10	9,21E-04	Probable peroxygenase 5	Calcium binding protein Caleosin
Solyc01g095340.2	-1,09	8,64E-04	Bag family molecular chaperone regulator 6	Unknown Protein
Solyc05g014280.2	-1,09	5,50E-05	Small heat shock chloroplastic-	Heat shock protein
Solyc06g053260.1	-1,08	5,10E-06	Auxin-induced protein x15-	Auxin-responsive family protein
Solyc00g136560.2	-1,08	2,61E-04	Unknown Protein	Undecaprenyl pyrophosphate synthase
Solyc08g079420.2	-1,07	6,62E-05	Geraniol 8-hydroxylase-	Cytochrome P450
Solyc07g061890.1	-1,07	1,55E-03	PREDICTED: uncharacterized protein LOC101255221	Unknown Protein
Solyc02g089510.2	-1,07	2,86E-03	Zinc finger protein constans-	Unknown Protein
Solyc01g105660.2	-1,06	5,86E-05	Probable 2-oxoglutarate fe - dependent dioxygenase	1-aminocyclopropane-1-carboxylate oxidase
Solyc01g104110.2	-1,06	3,66E-04	13s globulin seed storage protein 2-	Legumin 11S-globulin
Solyc11g008440.1	-1,05	2,94E-04	Vacuolar amino acid transporter 1-	Amino acid transporter
Solyc01g103650.2	-1,05	1,20E-05	Embryogenesis-associated protein emb8-	Hydrolase alpha/beta fold family
Solyc06g008300.2	-1,03	4,47E-04	Low quality protein: probable leucine-rich repeat receptor-like protein kinase at1g35710	LRR receptor-like serine/threonine-protein kinase%2C RLP
Solyc03g033410.2	-1,03	9,21E-05	Ubiquitin-conjugating enzyme e2 10-	Ubiquitin-conjugating enzyme E2 10
Solyc11g066250.1	-1,03	7,18E-05	Serine carboxypeptidase-	Serine carboxypeptidase
Solyc07g042630.2	-1,03	1,36E-05	Lupeol synthase	Beta-Amyrin Synthase
Solyc06g073500.2	-1,02	4,31E-04	Pentatricopeptide repeat superfamily protein isoform 2	Unknown Protein
Solyc00g050130.1	-1,02	1,93E-03	Unknown Protein	UDP-glucose glucosyltransferase
Solyc06g068600.2	-1,01	1,85E-05	Abc transporter i family member 17	Phosphate import ATP-binding protein pstB 1
Solyc06g062460.2	-1,00	1,35E-04	Transcription factor bhlh87-	BHLH transcription factor-like
Solyc06g051940.2	-1,00	2,72E-04	Probable protein phosphatase 2c 51	Protein phosphatase 2C
Solyc12g044950.1	-0,99	1,82E-03	Omega-6 fatty acid	Omega-6 fatty acid desaturase

			endoplasmic reticulum isozyme 2-	
Solyc05g013630.1	-0,99	1,70E-04	Cp-interacting protein-l	Unknown protein (Fragment)
Solyc12g019740.1	-0,99	9,18E-04	Thioredoxin-like 1- chloroplastic	Thioredoxin family protein
Solyc08g069060.2	-0,99	4,49E-04	Beta- -galactosyltransferase 7-	Beta-1 3-galactosyltransferase 6
Solyc06g053670.1	-0,98	3,79E-04	Enoyl- hydratase domain-containing protein mitochondrial-	Enoyl-CoA hydratase/isomerase family protein
Solyc06g051020.2	-0,98	2,95E-05	Peptide-n4-(n-acetyl-beta-glucosaminyl)asparagine amidase a-	Peptide-N4-(N-acetyl-beta-glucosaminyl)asparagine amidase A
Solyc04g007540.1	-0,97	3,01E-04	Mate efflux family protein 5-	Multidrug resistance protein mdtK
Solyc02g079960.2	-0,97	3,65E-04	Thioredoxin-like protein cxxs1	Thioredoxin h
Solyc04g053130.2	-0,97	1,30E-05	Stress enhanced protein chloroplastic	LHC-related protein
Solyc08g028690.2	-0,96	2,85E-04	Secoisolariciresinol dehydrogenase-	Tasselseed2-like short-chain dehydrogenase/reductase (Fragment)
Solyc03g116570.2	-0,96	1,43E-04	Dcc family protein chloroplastic	YuxK
Solyc03g098000.2	-0,96	1,12E-03	Alanine--trna ligase	At1g32160/F3C3_6
Solyc02g079430.2	-0,95	2,46E-04	Zinc finger protein constans-	CONSTANS-like zinc finger protein
Solyc04g074850.2	-0,95	7,72E-05	Protein transparent testa 12-	Multidrug resistance protein mdtK
Solyc09g089730.2	-0,95	1,55E-03	1-aminocyclopropane-1-carboxylate oxidase homolog	1-aminocyclopropane-1-carboxylate oxidase-like protein
Solyc02g063440.2	-0,95	1,64E-03	Unknown Protein	Unknown Protein
Solyc01g102960.2	-0,94	2,14E-03	Kda class iv heat shock	class IV heat shock protein
Solyc03g112060.2	-0,94	9,18E-04	Quinolinate chloroplastic	Quinolinate synthase A
Solyc04g072240.2	-0,94	1,06E-04	Uncharacterized oxidoreductase at4g09670	Oxidoreductase family protein
Solyc11g066740.1	-0,94	7,41E-04	Protein reticulata-related chloroplastic	Os12g0283800 protein (Fragment)
Solyc02g083280.2	-0,93	7,48E-04	Thiosulfate sulfurtransferase chloroplastic-	Thiosulfate sulfurtransferase/rhodanese-like domain-containing protein 1
Solyc09g074550.2	-0,92	1,50E-03	Casp-like protein 1e2	UPF0497 membrane protein 6
Solyc03g116700.2	-0,92	3,48E-04	Cucumber peeling cupredoxin-	Blue copper protein
Solyc02g078210.2	-0,92	6,78E-05	Probable ubiquitin-conjugating enzyme e2 24	Ubiquitin-conjugating enzyme 22
Solyc06g019170.2	-0,92	7,95E-04	Delta-1-pyrroline-5-carboxylate synthase-	Gamma-glutamyl phosphate reductase
Solyc04g076980.2	-0,91	1,49E-04	Receptor-like protein kinase haiku2	LRR receptor-like serine/threonine-protein kinase%2C RLP
Solyc01g080870.2	-0,91	1,80E-04	Protein nrt1 ptr family -	Peptide transporter-like protein

Solyc01g099750.2	-0,90	9,22E-04	Heparan-alpha-glucosaminide n-acetyltransferase	Heparan-alpha-glucosaminide N-acetyltransferase
Solyc04g009960.2	-0,90	1,01E-04	Probable low-specificity l-threonine aldolase 1	L-allo-threonine aldolase
Solyc03g114150.2	-0,90	1,52E-04	Aldehyde dehydrogenase family 2 member mitochondrial	Aldehyde dehydrogenase
Solyc03g006410.2	-0,90	7,75E-04	PREDICTED: uncharacterized protein LOC101259314	Plant-specific domain TIGR01615 family protein
Solyc12g042380.1	-0,89	6,24E-04	19-like isoform 2	MtN19-like protein
Solyc10g080610.1	-0,89	1,74E-03	F-box kelch-repeat protein at1g15670-	Kelch-like protein 14
Solyc04g025040.1	-0,88	7,27E-04	Rna-binding protein fus-	Unknown Protein
Solyc10g007070.2	-0,88	2,41E-03	Early nodulin-like protein 2	CT099 (Fragment)
Solyc08g076450.2	-0,88	9,89E-04	Nad -binding rossmann-fold superfamily protein isoform 1	3-beta hydroxysteroid dehydrogenase/isomerase family protein
Solyc02g068080.2	-0,88	5,57E-04	Chloride channel protein clc-b	Voltage-gated chloride channel
Solyc05g010040.2	-0,86	1,02E-03	PREDICTED: uncharacterized protein LOC102591126	Unknown Protein
Solyc04g079410.2	-0,86	2,80E-03	Protein mitochondrial-	Single-stranded DNA binding protein
Solyc05g005920.2	-0,86	5,80E-04	Protein nrt1 ptr family -	Peptide transporter
Solyc09g075020.2	-0,83	2,78E-03	Abc transporter c family member 14-	Multidrug resistance protein ABC transporter family
Solyc07g052950.2	-0,83	4,98E-04	PREDICTED: uncharacterized protein LOC101268883	Unknown Protein
Solyc07g062970.2	-0,83	7,49E-04	Probable protein phosphatase 2c 39	Serine/threonine phosphatase family protein
Solyc02g030300.2	-0,83	1,81E-04	G-type lectin s-receptor-like serine threonine-protein kinase at4g27290	Serine/threonine-protein kinase receptor
Solyc12g089220.1	-0,83	4,18E-04	Bifunctional nuclease 1-	Wound responsive protein (Fragment)
Solyc12g042470.1	-0,83	3,91E-04	Methylecgonone reductase-	Reductase 2
Solyc07g063910.2	-0,83	7,78E-04	PREDICTED: uncharacterized protein LOC101264952	Unknown Protein
Solyc11g069450.1	-0,83	1,04E-03	PREDICTED: uncharacterized protein LOC101259309	Arabidopsis thaliana genomic DNA chromosome 5 P1 clone MOK16
Solyc02g081550.2	-0,82	1,89E-03	Atp-dependent zinc metalloprotease ftsh chloroplastic-	ATP-dependent Zn protease cell division protein FtsH homolog
Solyc05g006740.2	-0,82	5,61E-04	Glutathione s-transferase u17-	Glutathione S-transferase
Solyc07g062060.2	-0,82	4,34E-04	Peptide methionine sulfoxide reductase chloroplastic	Peptide methionine sulfoxide reductase msrB
Solyc02g065000.1	-0,82	9,35E-04	Calmodulin-like protein 1	Calmodulin-like protein
Solyc04g017720.2	-0,80	2,90E-03	Protein gast1-	Gibberellin regulated protein

Solyc08g074490.2	-0,80	1,27E-03	Calcium-dependent protein kinase	Regulatory protein
Solyc06g074940.2	-0,80	8,53E-04	Abc transporter f family member 1-	ATP-binding cassette protein
Solyc03g112640.2	-0,79	1,57E-03	Sec14p-like phosphatidylinositol transfer family protein isoform 1	CRAL/TRIO domain containing protein
Solyc09g061840.2	-0,79	9,93E-04	3-ketoacyl- thiolase peroxisomal-	3-ketoacyl CoA thiolase 1
Solyc09g010140.1	-0,78	2,23E-03	Probable protein kinase ddb_g0277539-	Arabidopsis thaliana genomic DNA chromosome 5 P1 clone MOK16
Solyc05g008290.2	-0,77	1,34E-03	Multicopper oxidase lpr1-	Bilirubin oxidase
Solyc12g015630.1	-0,77	1,59E-03	PREDICTED: uncharacterized protein LOC101246694	Genomic DNA chromosome 5 P1 clone MDF20
Solyc10g078590.1	-0,76	7,17E-04	PREDICTED: uncharacterized protein LOC101247272	Unknown Protein
Solyc08g082640.2	-0,75	8,05E-04	Cellulose synthase-like protein g3	Cellulose synthase
Solyc04g040210.2	-0,75	2,07E-03	Cysteine-rich and transmembrane domain-containing protein a	Unknown Protein
Solyc03g117810.2	-0,75	3,87E-04	Abc transporter i family member 17	Phosphate import ATP-binding protein pstB 1
Solyc09g075060.2	-0,74	4,98E-04	Beta-glucosidase 11-	Beta-glucosidase
Solyc04g007780.2	-0,73	6,81E-04	Pr-10 type pathogenesis-related protein	Major latex-like protein
Solyc08g075370.2	-0,73	6,55E-04	Unknown Protein	Unknown Protein
Solyc03g095620.2	-0,72	9,40E-04	Uncharacterized aarf domain-containing protein kinase chloroplastic	ABC-1 domain protein
Solyc12g014100.1	-0,72	1,59E-03	Homogentisate -dioxygenase	Homogentisate 1 2-dioxygenase
Solyc05g050110.2	-0,72	2,02E-03	PREDICTED: uncharacterized protein LOC101254096	cDNA clone J013073A18 full insert sequence
Solyc11g013120.1	-0,72	2,75E-03	Upf0695 membrane protein -	Protein crcB homolog
Solyc10g005370.2	-0,71	1,45E-03	Probable phosphate dikinase regulatory chloroplastic	Pyruvate%2C phosphate dikinase regulatory protein 2
Solyc02g071280.2	-0,71	8,53E-04	16s rrna processing protein isoform 1	Ribosome maturation factor rimM
Solyc04g076820.1	-0,71	1,20E-03	Xin actin-binding repeat-containing protein	Octicosapeptide/Phox/Bem1p domain-containing protein
Solyc01g008070.2	-0,70	1,44E-03	PREDICTED: uncharacterized protein LOC101248126	Alpha/beta superfamily hydrolase
Solyc06g061090.2	-0,69	1,14E-03	Tld protein	LOC555512 protein (Fragment)
Solyc01g102860.2	-0,68	2,04E-03	PREDICTED: uncharacterized protein LOC101252228	Unknown Protein

Solyc07g065380.2	-0,68	1,35E-03	Zinc transporter 11	Zinc transporter 2
Solyc01g087030.2	-0,67	2,21E-03	Zinc finger ccch domain-containing protein 69-	Makorin RING finger protein
Solyc04g048900.2	-0,67	1,63E-03	Calreticulin-3-like isoform x1	Calreticulin 2 calcium-binding protein
Solyc03g112200.1	-0,66	2,42E-03	Hypothetical protein POPTR_0015s09570g	Unknown Protein
Solyc07g042190.2	-0,65	2,59E-03	Duf581 family protein	Os10g0422600 protein (Fragment)
Solyc05g052260.2	-0,64	2,27E-03	O-acetyl-adp-ribose deacetylase macrod2 isoform x1	Appr-1-p processing domain protein
Solyc07g006140.2	-0,63	2,32E-03	Cytochrome p450 cyp72a219-	Cytochrome P450