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Taciane FINATTO

Transcriptomic analysis of genes and LTR retrotransposons in rice (*Oryza sativa* ssp. *japonica*) in response to iron toxicity

Pelotas – Rio Grande do Sul - Brasil
2012

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"Análise transcriptômica de genes e LTR retrotransposons em arroz (*Oryza sativa* ssp. *japonica*) em resposta à toxidez por ferro"

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We especially need imagination in science. It is not all mathematics, not all logic, but it is somewhat beauty and poetry.

(Maria Montessori)

Dedico aos meus pais Ivete e Mário e aos meus irmãos Roberto e Franciel

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SUMMARY

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ABBREVIATIONS LIST

ABA	Abscisic Acid
ABC transporter	ATP-binding Cassette Transporters
AOX	Alternative Oxidase
APOBEC3	Apolipoprotein B mRNA-editing enzyme 3
APX	Ascorbate Peroxidase
ATPase	Adenosine Triphosphate Enzymes
bHLH	Helix-loop-helix
BP	Biological Processes
bp	Base pair(s)
Car	Carotenoids
cDNA	Complementary DNA
CDPK	Calmodulin-Domain Protein Kinase
ceNPB	Centromere Protein B
CRE	*cis*-Acting Regulatory Elements
cv	Cultivar
DBD	Dna-Binding Domain
DDM1	Decrease in DNA Methylation1
Dfr-B	Flower-Colour Gene
DHAR	Dehydroascorbate Reductase
DNA	Deoxyribonucleic Acid
DRM1	DDM1: DECREASE IN DNA METHYLATION1
dsDNA	Double Stranded Structure of DNA
dTok	Transposable Element
EDTA	Ethylenediamine Tetraacetic Acid
EN	Envelope
endo-siRNAs	A class of Small Short Interfering RNA
ERF	Ethylene-Responsive Factor
Fe	Iron
$Fe(OH)_3$	Iron Oxide-Hydroxide
Fe^{2+}	Ferrous Iron
Fe^{3+}	Ferric Iron
FER	Ferritin or Phytoferritin
$FeSO_47H_2O$	Ferrous Sulfate Heptahydrate
FRO	Ferric Chelate Reductase
FWA	Flowering activation
GAPDH	Glyceraldehyde 3-Phosphate Dehydrogenase
GPOX	Guaiacol Peroxidase
GPX	Glutathione Peroxidase
GR	Glutathione Reductase
GSH	Glutathione
GST	Gluthatione S-Transferase
GTF	General Transcription Factors
H_2O_2	Hydrogen peroxide
HAT	Histone acetyl-Transferase
HDAC2	Histone deacetylase

HSP	Heat Shock Protein
HTH	Helix-Turn-Helix
Hxk2	Hexokinase
IAP	Intracisternal A Particles
Inr	Initiator Element
INT	Integrase
IRT	Iron Related Rransporter
kbp	Kilobase pairs
KYP-CMT3	kryptonite- chromomethylase 3
L1	Long Interspersed Element 1
LINE	Long Interspersed Nuclear Elements
LOL1	LSD1 like 1-like
LPO	Lipid Peroxidation
LRR	Leucine Rich Repeat
LTR	Long terminal repeat
·OH	Hydroxyl Radical
MA	Mugineic acid family phytosiderophores
MAPK	Mitogen Activated Protein Kinase
MATE	Multi Antimicrobial Extrusion Protein (MATE)
MDHAR	Monodehydroascorbate reductase
met1	Methylation Mutants
MET1	METHYLTRANSFERASE1
MF	Molecular Functions
MITE	Miniature Inverted-Repeat Transposable Element
MKS	MAP Kinase Substrate
mRNA	Messenger RNA
MT	Metallothionein
Muk	Mu killer
MYB	Myeloblastosis protein
NA	Nicotianamine
NADPH	Nicotinamide Adenine Dinucleotide Phosphate
nDart	Transposable Element
NMD	Nonsense-mediated Decay
NMPP	NimbleGen Microarray Data Processing Pipeline
NRAMP	Natural Resistance Associated Macrophage Protein
O2-	Superoxide Radical
P450	Cytochrome P450 Monooxygenases
PC	Phytoquelatin
PEV	Position Effect Variegation
PG	Polygalacturonase
pH	Hydrogenionic potential
PI	Phosphatidylinositol
PLACE	Database of Plant *Cis*-Acting Regulatory DNA Elements
piRNAs	PIWI-interacting RNAs
POD	Peroxidase
Pol-II	Polymerase 2
PR	Protease
PR1a	Pathogenesis Related

pre-mRNA	Precursor of mRNA
Pro	Proline
PS	Phytosiderophore
PSI	Photosystem I
PSII	Photosystem II
RBOH	Respiratory Burst Oxidase
RISC	RNA-induced Silencing Complex
RLK	Receptor-Like Kinase
RNA	Ribonucleic Acid
RNAi	RNA interference
ROS	Reactive Oxygen Species
RT	Reverse transcriptase
RT-qPCR	Reverse transcriptase real time quantitative polymerase chain reaction
SIL1	SILENCING1 - histone deacetylase
SINE	Non-autonomous short interspersed elements
SOD	Superoxide Dismutase
Spm	Suppressor-Mutator
tb1	Teosinte Branched1
TCA	Citrate Cycle
TE	Transposable Element
TFs	Transcription Factors
TIP	Transposon Insertion Polymorphisms
TIR	Terminal Inverted Repeats
Tos17	Transposon of *Oryza sativa* 17
TPRT	Target-Site-Primed Reverse Transcription
TSD	Target-Site Duplication
TSS	Transcription Start Site
Ub	Ubiquitin
UTR	Untranslated Region
UV	ultra-violet
WAK	Wall associate Kinases
WRKY	Transcription factors that have a conserved zink finger and WRKY dominium
YGL1	*Oryza sativa* yellow-green leaf1/chlorophyll synthetase
YS	Yellow Stripe
YSL	Yellow Stripe-like
ZF	Zinc Finger
ZIP	Leucine Zipper

ABSTRACT

Iron toxicity in plants is associated with the presence of large concentrations of reduced iron (Fe^{2+}) in the soil solution, which occurs in flooded soils and affects rice plants grown under this condition. Symptoms of iron toxicity involve oxidative stress in leaves, as a response to excessive Fe^{2+} absorption by the roots. The responses of plants to stress conditions include stimulus perception, signal transduction and gene transcription activation. Besides gene expression, LTR (Long Terminal Repeat) retrotransposons represent ca. 22% of the rice genome, they can be transcriptionally activated under stress, and they can alter the expression of adjacent genes (e.g. due to alterations in chromatin structure). This study aimed to identify differentially expressed genes and LTR retrotransposons in leaves of 18-day-old rice seedlings (*Oryza sativa* ssp. *japonica* cv. Nipponbare) after four days of iron excess exposure. They were identified a differential expression of genes and LTR retrotransposons in rice exposed to iron excess using a microarray approach. Total RNA was extracted from leaves of 18-day-old rice seedlings (*Oryza sativa* L. ssp *japonica* cv. Nipponbare) after four days of cultivation in nutrient solution with iron excess (7 mM of $FeSO_4 7H_2O$) and in a control solution. The hybridization was performed with cDNA and rice transposome array v. 2.0 microarray (Roche/NimbleGen technology, an improvement of v.1.0, Picault et al., 2009). Data from gene expression was analyzed by the Bayesian *t*-test with BH adjustment method. Gene annotation, gene ontology, and LTR retrotransposon identification were performed at RAP-DB (Rice Annotation Project Database, build 5), and microarray results were validated by RT-qPCR. Considering $\log_2$ FC ($\log_2$-fold-change) $\leq$ -1 as underexpression and $\geq$ 1 as overexpression (p-values $\leq$ 0.05), 44 down-regulated and 1,572 up-regulated genes with described function were identified. Down-regulated genes were related to a wide range of functions and no gene family could be highlighted. Among the up-regulated genes, 166 were transcription factors, the most representative belonging to the Zinc finger RING/FYVE/PHD-type family (22) and WRKY family (19); other genes were from the kinase family, participating in biological processes of protein amino acid phosphorylation (86); had molecular function of iron ion binding (56); were involved in response to oxidative stress (scavenging of reactive oxygen species) (26); had molecular function of transport activity (84), including four genes related to heavy metal transport/detoxification and four genes of the multi antimicrobial extrusion protein MATE family; and were involved in the biological

process of apoptosis (14), including 10 genes of NB-ARC. Among the up-regulated genes, 435 present at least one *cis*-regulatory element responsive to abscisic acid (ABA) with significant occurrence ($P \leq 0.05$) in its promoter region (1 kbp upstream of the transcription start site). These data indicate that about 28% of the up-regulated genes can be regulated by changing in the ABA content in leaves in response to iron excess. Regarding expression of LTR retrotransposons, 302 were down-regulated (53 *Ty1/Copia*, 172 *Ty3/Gypsy* and 77 unclassified), and 4342 up-regulated (466 Ty1*/Copia*, 2276 *Ty3/Gypsy* and 1600 unclassified). They were observed a large activity of LTR retrotransposons in response to iron toxicity, and furthermore, they were verified that LTR retrotransposons transcription can extend to 5' and 3' flanking regions. In addition, 16 situations that should up-regulated LTR retrotransposons are located at a very short distance (smaller than 1000 base pairs) in the same chromosome of up-regulated genes suggesting co-transcription, these occurrences are represented by eight where the LTR retrotransposon and the gene have the same sense of transcription (plus); five occurrences with the both with the same sense of transcription (minus) and one occurrence where they have opposite senses. Additionally, two occurrences that in which both, DNA sequences of up-regulated retrotransposon and gene, are overlapped and have the same sense of transcription.

Key-words: Nipponbare, iron toxicity, oxidative stress, *cis*-regulatory elements, signaling cascade, *cis*-regulatory elements, abscisic acid, co-transcription LTR retrotransposon and genes, LTR retrotransposons flanking region transcription.

RESUMO

A toxidez por ferro em plantas está associada com a presença de grandes concentrações de ferro (Fe) reduzido (Fe^{2+}) na solução do solo, esta condição pode ocorrer em solos irrigados por inundação. Os sintomas de toxidez por ferro incluem estresse oxidativo nas folhas como resultado do excesso de Fe^{2+} absorvido pelas raízes, resultando em perdas na produtividade. As respostas das plantas às condições de estresse envolvem a percepção dos estímulos, transdução de sinais e ativação da transcrição gênica. Além da expressão gênica, os LTR retrotransposons (*Long Terminal Repeat* Retrotransposons) que respresentam cerca de 20% do genoma do arroz, podem ser transcricionalmente ativados em condições de estresse e desta forma, influenciar a expressão de genes adjacentes (por exemplo devido a alterações na estrutura da cromatina). Este estudo teve por objetivo identificar genes e LTR retrotransposons diferencialmente expressos em plântulas de arroz (*Oryza sativa* ssp. *japonica* cv. Nipponbare), após quatro dias de exposição ao excesso de ferro em solução nutritiva. A expressão diferencial de genes e LTR retrotransposons foi analisada utilizando a técnica de microarranjo e sua validação foi realizada por meio de RT-qPCR. O RNA total foi extraído de folhas de plântulas de arroz cv. Nipponbare, após quatro dias de cultivo em solução nutritiva adicionada de ferro na concentração de 7 mM ($FeSO_4 7H_2O$) (presença de toxidez) e a condição controle com presença de ferro na concentração de 10 µM. O cDNA fita dupla foi sintetitizado a partir do RNA mensageiro. A hibridização foi realizada entre o cDNA das duas condições em triplicatas biológicas e o microarranjo *Rice Transposome Array* v. 2.0 (Roche/NimbleGen technology, an improvement of v.1.0, Picault et al., 2009). Os valores de intensidade de cada *spot* foram normalizados, transformados e comparados pelo teste T Bayesiano. A identificação dos genes e LTR retrotransposons foi realizada de acordo com o banco de dados RAP-DB (*Rice Annotation Project Database, build 5*). Considerando $\log_2$ FC (log_2*-fold-change*) ≤ -1 como subexpressão e ≥ 1 como superexpressão e $P \leq 0.05$ para ambas condições. Foram identificados 44 genes subexpressos e 1.572 superexpressos com funções descritas. Os genes subexpressos desempenham a uma vasta gama de funções. Entre elas destacam-se: 166 genes que são fatores de transcrição, sendo que os mais representativos pertencem à família *Zinc finger* RING/FYVE/PHD-*type family* (22 genes) e WRKY (19 genes); outros genes da família das cinases que participam também da sinalização celular em processos biológicos de fosforilação de aminoácidos nas proteínas (86 genes); outros genes com função molecular de ligação ao íon ferro (56 genes); 26 genes envolvidos na resposta ao

estresse oxidativo (*scavengers* de espécies reativas de oxigênio); 84 genes com função molecular de transporte, incluindo quatro genes relacionados ao transporte e detoxificação de metais pesados e quatro genes da família MATE; 14 genes envolvidos em apoptose, incluindo 10 genes NB-ARC. Entre os genes superexpressos, 435 apresentam pelo menos um elemento regulatório de ação *cis* responsivo ao ácido abscisico (ABA) com ocorrência significativa ($P \leq 0,05$) em sua região promotora (1 kbp a montante do sítio de início da transcrição). Estes dados indicam que cerca de 28% dos genes superexpressos podem ser regulados pelas alterações no conteúdo de ABA nas folhas, em resposta ao estresse por excesso de ferro. Considerando a expressão do LTR retrotransposons, 302 apresentaram subexpressão (53 *Ty1/Copia*, 172 *Ty3/Gypsy* e 77 não classificados), e 4.342 apresentaram superexpressão (466 Ty1*/Copia*, 2276 *Ty3/Gypsy* e 1600 não classificados). Foi constatada grande atividade transcricional dos LTR retrotransposons em resposta à toxidez por ferro, sendo que a transcrição dos LTR retrotransposons pode se estender às suas regiões flanqueadoras 5' e 3', além disso foram encontradas 16 ocorrencias em que o LTR retrotransposon e o gene superexpresso estão localizados a uma distância menor do que 1000 pares de bases no mesmo cromossomo, sugerindo co-transcrição entre ambos. Entre as 16 ocorrências, oito em que o LTR retrotransposon e o gene apresentam o mesmo sentido de transcrição (*plus*); cinco ocorrências com mesmo sentido de transcrição (*minus*) e uma ocorrência onde LTR retrotrotransposon e gene apresentam sentidos de transcrição opostos. Foram observadas ainda, duas ocorrências em que as sequencias de DNA do LTR retrotransposon e do gene superexpressos estão sobrepostas, e apresentam o mesmo sentido de transcrição.

Palavras-chave: Nipponbare, toxidez por ferro, estresse oxidativo, cascata de sinalização, elementos regulatórios de ação *cis*, ácido abscísico, co-trancrição LTR retrotransposons e genes; transcrição das regiões flanqueadoras dos LTR retrotransposons.

GENERAL INTRODUCTION

Oryza sativa L. is the staple food of more than two thirds of the world´s population, it is the second most widely grown cereal in the world, and Brazil is the largest producer outside Asia (nineth position) (FAOSTAT, 2010). There are two distinct types of domesticated rice, *Oryza sativa* or Asian rice and *Oryza glaberrima* or African rice that are grown globally (Sweeney and McCouch, 2007).

Asian rice, *O. sativa*, and the African rice, *O. glaberrima* are thought to be an example of parallel evolution in crop plants. The wild progenitor of *O. sativa* is the Asian common wild rice, *O. rufipogon*, which shows a range of variation from perennial to annual types. Annual types, also given a specific name of *O. nivara*, were domesticated to become *O. sativa*. In a parallel evolutionary path, *O. glaberrima* was domesticated from annual *O. breviligulata*, which in turn evolved from perennial *O. longistaminata* (Khush, 1997) (Figure 1).

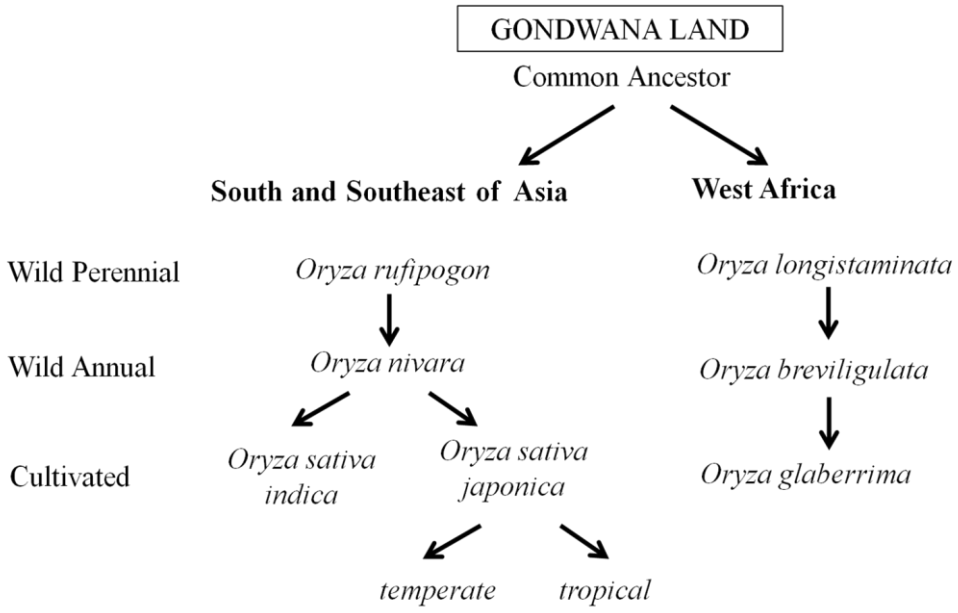

Figure 1. Evolutionary pathway of two cultivated species of rice. Source: Khush, 1997.

A phylogeographic study suggested that *indica* was domesticated within a region south of the Himalayan mountain range including eastern India, Myanmar, and Thailand, whereas *japonica* was originated from southern China (Londo et al., 2006). Additionally, data suggest that cultivated rice was domesticated at least twice from different *O. rufipogon* populations and that the products of these two independent domestication events are the two major rice varieties, *Oryza sativa indica* and *Oryza sativa japonica*. The time of the

separation has been estimated as more than 100,000 years ago. This date precedes domestication, supporting independent domestications of *indica* and *japonica* from pre-differentiated pools of the wild ancestor (Sweeney and McCouch, 2007).

The genus *Oryza* contains 21 wild relatives of the domesticated rices. The genus is divided into four species complexes: the *O. sativa*, *O. officialis*, *O. ridelyi* and *O. granulata* species complexes. All members of the *Oryza* genus have n=12 chromosomes and while interspecific crossing is possible within each complex, it is difficult to recover fertile offspring from crosses across complexes (Vaughan et al., 2003).

The *O. sativa* complex contains two domesticated species: *O. sativa* and *O. glaberrima*, and five or six wild species: *O. rufipogon*, *O. nivara* (also considered to be an ecotype of *O. rufipogon*), *O. barthii*, *O. longistaminata*, *O. meridionalis* and *O. glumaepatula*, all of which are diploids. *Oryza sativa* is distributed globally with a high concentration in Asia, while *O. glaberrima* is grown in West Africa. *Oryza rufipogon* can be found throughout Asia and Oceania. *Oryza barthii* and *O. longistaminata* are African species, *O. barthii* endemic in West Africa and *O. longistaminata* is found throughout Africa. *Oryza meridionalis* is native to Australia and *O. glumaepatula* is endemic in Central and South America (Sweeney and McCouch, 2007).

Oryza sativa represent the genome model among the monocots, which has a small genome (~389 Mbp) and was sequenced for variety Nipponbare *O. sativa* ssp. *japonica* (Goff et al., 2002 and IRGSP, 2005) and for variety 93 -11 *O. sativa* ssp. *indica* (Yu et al., 2002). *O. sativa* actually has databases continuously updated with advanced gene annotation with descrition of gene function, aminoacid sequences and gene ontology.

Irrigated rice, *O. sativa* ssp *indica* is a crop of large importance in the state of Rio Grande do Sul (Brazil), accounting for over half of total production in the country. Iron (Fe) is an essential micronutrient for plant growth (Sachs, 1860; Marschner, 1995). In irrigated conditions, due to the anaerobic conditions present, the Fe^{3+} ions are reduced to Fe^{2+} that can be easily absorbed by the rice plants. When rice is under conditions of excess iron in the soil, symptoms of toxicity are observed in leaves.

Iron (Fe) is essential for most life, but it also readily engages in one-electron reduction-oxidation (redox) reactions between its ferric ($^{3+}$) and ferrous ($^{2+}$) states that can catalyze the generation of toxic free radicals through the Fenton reaction (Pierre and Fontecave, 1999).

In irrigated conditions, due to the anaerobic conditions present, the Fe^{3+} ions are reduced to Fe^{2+} that can be easily absorbed by the rice plants. When rice is under conditions of excess iron in the soil, symptoms of toxicity are observed in leaves that culminates with losses in crop production in sensitive cultivars. One major symptom is called bronzing, which is generated by direct toxicity (due to excessive absorption of iron), another phenomenon observed is the orange color in the leaves, caused by indirect toxicity, where there is the formation of a layer of iron hydroxides on the root surface which prevents the absorption of micronutrients, including iron itself (Vahl, 1991; Mengel and Kirkby, 1982; Bienfait, 1985; Wan et al. 2004).

Rice plants have developed morphological and physiological mechanisms for avoidance and/or tolerance mechanisms to cope with and survive adverse iron-toxic soil conditions and large amounts of iron in the plant (Becker and Asch, 2005). Three major types of adaptation strategies can be differentiated. Strategy I (exclusion/avoidance) plants exclude Fe^{2+} at the root level and hence avoid of Fe^{2+} damage to the shoot tissue (rhizospheric oxidation and root ion selectivity). Strategy II (inclusion/avoidance) the Fe^{2+} is taken up into the rice root, but tissue damage may be avoided by either compartmentalization (immobilization of active iron in "dumping sites", e.g., old leaves or photosynthetically less active leaf sheath tissue) or exclusion from the symplast (immobilization in the leaf apoplast), and finally, strategy III (inclusion/tolerance) when the plants actually tolerate elevated levels of Fe^{2+} within leaf cells, probably via enzymatic "detoxification" in the symplast (Becker and Asch (2005).

Recently, several studies aiming to identify genes responsive to stress by iron toxicity have been described, however, in the literature there is a predominance of studies on iron deficiency. Regarding the toxicity of iron, studies have been conducted primarily for differential expression of target genes, such as genes related to iron transport such as *OsIRT* (Lee an An, 2009), *OsNRAMP1 e OsNRAMP2* (Zhou and Yang, 2004; Soares-Bresolin, 2010), storage proteins such as ferritin (*OsFER*) (Silveira et al., 2009), genes responsive to oxidative stress generated by excessive absorption of iron such, ascorbate peroxidase, and the transcription factor *OsWRKY8*0 (Ricachenevsky et al. 2010), *OsFDRL1* (Soares-Bresolin, 2010). Dufey et al. (2009) identified a total of 24 putative QTLs on chromosomes 1, 2, 3, 4, 7 and 11 for leaf index bronzing and other traits related to iron toxicity tolerance. The response to iron toxicity is a feature that depends of the interaction between many genes, and different

genotypes presents different degrees of tolerance/susceptibility in different stages of development.

Transposable elements (TEs) are mobile DNA sequences in the genome and were described for the first time by Barbara McClintock (in the 50s). The LTR retrotransposons (long terminal repeat) belong to Class I, where TEs transpose via RNA by a mechanism of "copy and paste", where a new copy of the element is integrated into a new position in the genome. LTRs and are the main components of most plant genomes. Near 40% of the rice genome is composed of TEs, of these 22% are LTR retrotransposons (Ma et al. 2004).

Although most TEs are transpositionally inactive, they can be activated by stress (McClintock, 1984). The existence of TEs transpositionally active in rice was demonstrate for *Tos 17* (Hirochika et al. 1996), the LINE (Long Interspersed Nuclear Elements) Karma (Komatsu et al. 2003), *dTok* (Moon et al., 2006), *nDart* (Tsugane et al., 2006), mPing/Pong (Jiang et al. 2003) and Lullaby (Picault et al., 2009).

The transcriptional or transpositional activation of the LTR retrotransposons can significantly alter the expression of genes, which may lead to gene silencing, or can alter the expression of adjacent genes. It has been demonstrated in wheat, where the activation of *Wis 2-1A* retrotransposon leads to the synthesis of new transcripts from adjacent sequences (Kashkush et al. 2003). It was also shown that the expression of *Tnt1* tobacco retrotransposon is related to hormonal defence signals triggered by a pathogen (Grandbastien et al. 1997).

The transcriptional activation of LTR retrotransposons can lead to the expression of adjacent genes, as has been demonstrated in wheat, where the activation of *Wis 2-1A* retrotransposon leads to the synthesis of new transcripts from adjacent sequences. Sequences can be in sense or antisense orientation of known genes. Activation of the sense or antisense transcripts associated with the activation or inactivation of the corresponding genes, respectively. In this way considering the abundance of LTR retrotransposons in genomes and their ability to be activated by different signals, it possible that TEs may be control elements of gene expression (Kashkush et al. 2003).

The microarray is a technique that allows measure the gene expression changes monitoring the expression levels in cells for thousands of genes simultaneously (Yang et al., 2001). The first report of the use of DNA microarrays came in 1991, with the publication of the chemical synthesis of oligonucleotides on glass chips by Fodor et al. (1991). In a typical microarray experiment utilizing ‘spotted arrays’, the two mRNA samples to be compared are

reverse transcribed into cDNA (Taniguchi et al., 2001), subsequently both, direct as well as indirect labelling protocols are applied: either, one target cDNA is labelled with a single dye and hybridized on a microarray slide, or two targets are labelled with two different dyes, one for the reference and one for the test sample, and co-hybridized on a microarray slide. In dual label experiments, most often Cyanine 3 (Cy3) and Cyanine 5 (Cy5) are used as fluorescent dyes, although other dyes have been suggested (Cox et al., 2004). The intensity values generated from hybridization to individual DNA spots are indicative of gene expression levels, and comparisons in gene expression levels between the two samples are derived from the resulting intensity ratios (Taniguchi et al., 2001). In this way differential expression for thousands of genes between two different RNA samples can be measured simultaneously (Staal et al., 2005).

Based on the exposed above, this thesis aimed to verify the transcriptional profile of genes and LTR retrotransposons in leaves of 18-day-old rice seedlings (*Oryza sativa* ssp. *japonica* cv. Nipponbare) after 4 days of exposure to iron excess (7 mM of Fe as source $FeSO_4.7H_2O$) using a cDNA microarray approach. Nipponbare was chosed because presents genome sequenced, the microarray was designed based on sequences of this cultivar and Nipponbare is a cultivar characterized as tolerant to iron excess by Wan et al. (2003).

This thesis is divided into five chapters. The first two concern to bibliographic support and the others 3 chapters concern to methodology, results and discussion.

The chapter I deals with the toxicity of iron and the response of plants to this stress condition. The chapter II is about the TEs and its relation with the the host genome, how they are maintained inactive/silenced or possible activation transpostional and transcriptional face certain enviromental conditions. The chapter III addresses to the methodology that was utilized. The chapter IV presents the results and discussion and is subdivided in three parts: first part reports the down and up-regulated genes responsive to iron toxicity, gene ontology and pathways that these genes are involved; second part is the results of significant occurrence of *cis*-regulatory elements in promoter of up-regulated genes and identification of genes responsives to abscisic acid (the plant stress hormone); and third part reports the expression of LTR retrotransposons down and up-regulated, putative co-transcripton with nearby (<1000 pb of distance) genes and the expression profile of LTR retrotransposons flanking regions. The chapter V presents a general discussion that connects the results and proposes a model of response to iron toxicity in Nipponbare.

CHAPTER I

IRON TOXICITY AND PLANT RESPONSES

1.1 *Iron Function in Plants*

Iron is an essential element for living organisms because of its physicochemical properties and is able to form six coordinated links with electron donor atoms such as oxygen or nitrogen (Marschner, 1995). As a consequence, it is found associated to a huge range of metalloprotein active sites, under the form of various prosthetic groups including heme and [Fe–S] clusters. Its best known function is, however, its structural role in the prosthetic groups of enzyme systems such as cytochromes, catalases and peroxidases. These enzymes are also the main components of the chloroplast and mitochondria (Marschner, 1995; Mengel and Kirby, 1987). The cytochrome acts essentially as an electron carrier in the respiratory chain. Iron interacts also with non-heme proteins such as those proteins in the iron sulfide group (ferredoxin, superoxide dismutase) and is also active in proteic synthesis. In thylacoidal membranes about 20 iron atoms are directly active in PSII and PSI electron transport (Audebert, 2006).

1.2 *Iron in the Soil*

The concentration of iron in the soluble phase of soils is determined by the rate of dissolution versus precipitation of oxides and hydroxides according to the reaction $Fe(OH)_3$ + Fe(III) + $3OH^-$. The equilibrium state of this reaction is strongly dependent of the pH of the soil solution. Iron disponibility in solution decreases when pH increases, reaching a minimum for pH values ranging to 7.4 to 8.5 (Lindsay and Schwab, 1982). Furthermore, iron solubility is also influenced by (i) redox conditions of the soil, (ii) properties of the solid mineral: solubility increases as particle sizes decrease, and (iii) presence of organic matter: organic chelates such as bacterial siderophores (Neilands et al., 1987), plant root exudates (Takagi, 1976), or humic substances (Stevens on, 1994) increase iron solubility.

1.3 *Iron Uptake and Transport by Plants*

Higher plants have evolved two strategies for Fe acquisition. The reduction strategy, Strategy I, with the exception of the grasses, is employed by all the plant species. The Strategy I approach involves pumping protons by H^+-ATPases to acidify the rhizosphere and increase Fe solubility in the soil. A ferric chelate reductase (FRO) reduces Fe^{3+} to Fe^{2+}, and Fe^{2+} transporters (IRTs) transport Fe into cells (Kim and Guerinot, 2007; Walker and Connolly, 2008; Giehl et al., 2009). Grass plants use the chelation strategy (Strategy II) (Kim

and Guerinot, 2007; Walker and Connolly, 2008). Grass plants synthesize and release mugineic acid family phytosiderophores (MAs) from their roots to chelate Fe^{2+} (Figure 1.1). The Fe^{3+}-MA complexes are then taken up through Fe^{3+}–MA transporters (Curi e et al., 2001; Murata et al., 2006; Lee et al., 2009). Ishimaru et al. (2006) verified that rice, exceptionally, in addition to absorbing a Fe^{3+}-phytosiderophore (strategy II), possesses a Fe-uptake system that directly absorbs the Fe^{2+} (strategy I). This is advantageous for growth in submerged conditions because unlike other grasses, rice is well adapted to grow in flooded conditions where the Fe^{2+} is more abundant than Fe^{3+}.

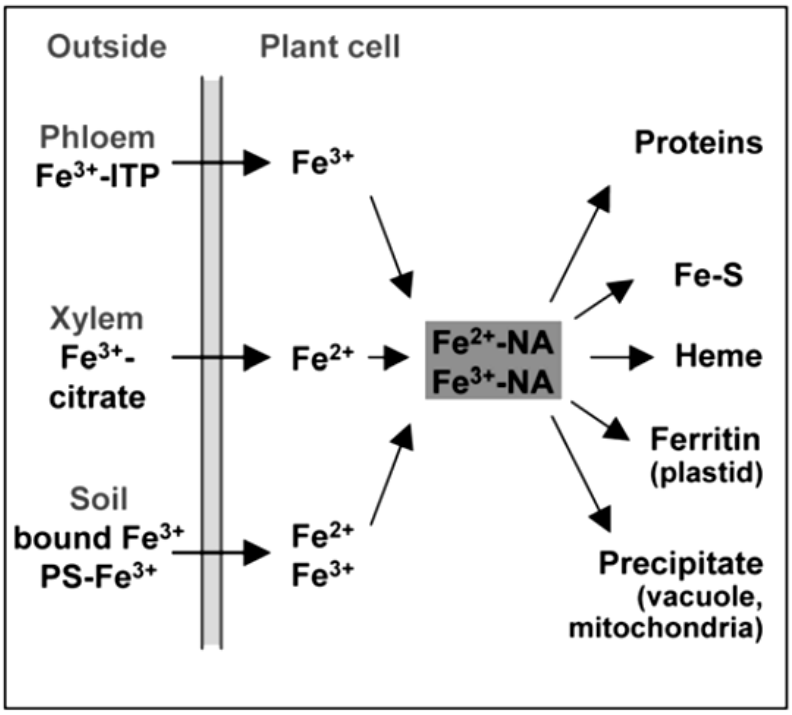

Figure 1.1 Simplified model of nicotianamine (NA) function in plant cells. Iron is transported across the plasma membrane (grey bar) by the strategy I or strategy II uptake systems. Inside the cell, NA is the default chelator of iron to avoid precipitation and catalysis of radical oxygen species. Proteins, the iron–sulfur cluster and heme are the main functional targets, while ferritin and iron precipitates are only present during iron excess. Note that only iron species outside and inside are indicated, but not the actual membrane transport systems. Since NA is present in the xylem and phloem, NA–iron complexes might represent a transport species in strategy I and II plants using YS-like transporters. Source: Hell and Stephan (2003).

Rice plants have the tendency of taking up more iron than most other plants, and Fe^{2+} is the iron species prevailing in paddy fields. Since Fe^{2+} is easily taken up, the uptake mechanism of Fe^{2+} is probably of less importance in flooded environments (Mengel, 1972). After uptake into the root cortex, the reduced Fe^{2+} can enter the xylem after a symplastic

passage through the Casparian strip. However, a large share of Fe^{2+} may enter the xylem directly via an apoplastic bypass (shown for sodium by Ye et al., 1987; Tsuchiya et al., 1995; Asch, 1997). In the xylem, Fe^{2+} follows the transpiration stream in the acropetal long-distance transport (Becker and Asch, 2005).

Iron reactivity with oxygen has a negative consequence for plants. Iron - mediated oxidative stress, through the Fenton reaction can lead to aminoacid oxidation, lipid peroxidation, and DNA mutations, ultimately causing cell death (Briat, 2002, 2007).

In cells, free Fe^{2+} is toxic because it is able to catalyze the decomposition of H_2O_2 to the extremely reactive hydroxyl (·OH) radical. This is known as the Fenton reaction. The resulting Fe^{3+} can be reduced back to Fe^{2+} by the superoxide radical (O), regenerating Fe^{2+} and allowing the reaction to continue. The sum of these two reactions is known as the Haber–Weiss reaction (Scheme 1), while the Fenton reaction without iron is slow, the reaction is enhanced greatly in the presence of iron (Halliwell and Gutteridge 1984, 1989; Rush et al. 1990).

Fenton reaction: $H_2O_2 + Fe^{2+}/Cu+ \rightarrow \bullet OH + OH^- + Fe^{3+}=Cu^{2+}$

$^{\cdot}O\_2 + Fe_{3+} = Cu^{2+}\ Fe^{2+}/Cu^{2+}$

Haber–Weiss reaction: $H_2O_2 + \bullet O_2 \rightarrow OH + OH^- + O_2$

Regarding iron transporters, Narayanan et al. (2006) has used a specialized macroarray that provided a short list of potential candidate genes, expressed in leaves, which might contribute to the process of metal transport to distant sinks, such as seeds. Flag leaves were evaluated because are the major source of phloem-delivered photoassimilates and remobilized metals for developing seeds. The expression of metal-related genes in flag and non-flag leaves of four different rice cultivars (Cocodrie, Taipei 309, IR58, and IR68144) were analyzed during the period of mid-grain fill. It was observed that 12 genes (*OsIRT1, OsZIP1, OsZIP5, OsZIP8, OsYSL5, OsYSL6, OsYSL7, OsYSL8, OsYSL18, OsNRAMP2, OsNRAMP4* and *OsNRAMP7*) were found to be highly expressed in both flag and non-flag leaves of all four cultivars.

1.4 *Adaptation Strategy to Iron Toxicity by Plants*

To cope and survive with adverse iron toxic soil conditions and large amounts of iron in the plant tissue, rice plants have developed morphological and physiological mechanisms of avoidance and/or tolerance. These mechanisms are important in the selection of tolerant or adapted rice genotypes. Three major types of adaptation strategies in rice can be differentiated and were highlighted by Becker and Ash (2005), these strategies comprise "includer" and "excluder" well as "avoidance" and "tolerance" mechanisms (Figure 1.2).

Plants employing strategy I (exclusion/avoidance) exclude Fe^{2+} at the root level and hence avoid of Fe^{2+} damage to the shoot tissue (rhizospheric oxidation and root ion selectivity) (Ando, 1983). In this case occurs the oxidation of iron at the root surface, Fe^{2+} formed either in situ in the soil or imported via interflow, must first pass the oxidation barrier in the rhizosphere before being absorbed by the root. To establish this barrier, molecular oxygen is channeled from the atmosphere through the stems into the roots via a gas-conducting tissue or aerenchyma. This aerenchyma forms upon the establishment of anoxic conditions which induce an increased production of ethylene (Kawase, 1981). Another form of exclusion is root membrane selectivity; in this case, reduced iron having passed the oxidative barrier of the rhizosphere enters the root apoplast. Reduced iron can be excluded at the root cell membranes (Tadano, 1976), explaining the Fe^{3+} deposition in the apoplast of root parenchymatic cells as observed by Green and Etherington (1977). Xylem-sap analysis of two-months-old rice plants indicated that up to 87% of the Fe reaching the root apoplast by mass flow was not detected in the xylem and must hence have been "excluded" at the endodermal barrier between cortex and stele (Yamanouchi and Yoshida, 1981).

Plants with strategy II (inclusion/avoidance), Fe^{2+} is taken up into the rice root, but tissue damage may be avoided by either compartmentation (immobilization of active iron in "dumping sites" e.g., old leaves or photosynthetically less active leaf sheath tissue) or exclusion from the symplast (immobilization in the leaf apoplast). This kind of strategy consists in the retention of iron in root and stem tissues (Tadano, 1976). The Fe^{2+} that has entered the xylem stream will follow the transpiration-driven acropetal long-distance transport. Some "metabolic inactive" Fe has been found inside the root tissue (Tanaka et al., 1966). The rice plants' ability to retain iron inside the root reportedly decreases with plant age (Tadano, 1976). During the further acropetal transport, Fe^{2+} may be immobilized and deposited in stem/leaf sheath tissues. Iron-tolerant cultivars from West Africa transported less

iron from the roots into the leaf blades, whereas the iron content of the leaf sheath substantially increased (Audebert and Sahrawat, 2000), possibly involving both, immobilization or re-oxidation of Fe^{2+}. This "withdrawal" of active Fe may involve the formation of ferritin in the xylem and its subsequent storage in stem tissues (Seckbach, 1982; Smith, 1984). The second possibility is the retention in the apoplast of the leaf. The apoplastic pH is hypothesized to largely determine the mobility of iron in leaves (Kosegarten et al., 1999). An acidic apoplastic pH will favor the uptake of Fe^{2+}. In plants unable to regulate apoplastic pH or reduce the activity of the Fe^{3+} reductase, an uncontrolled accumulation or influx of Fe^{2+} in the leaf cell can occur (Welch et al., 1993).

Strategy III plants (inclusion/tolerance) actually tolerate elevated levels of Fe^{2+} within leaf cells, probably via enzymatic "detoxification" in the symplast (Yamanouchi and Yoshida, 1981). Whereas Fe^{2+} exclusion by oxidation in the rhizosphere and the detoxification of radicals in leaf cells are well established Fe-tolerance mechanisms of rice, the other mechanisms are not yet well understood and have not been considered in rice breeding or screening for iron tolerance (Becker and Asch, 2005).

The strategy III consists in symplastic tissue tolerance, once it has entered the symplast, Fe^{2+} will catalyze the generation of ROS. Prevention of oxidative damage and detoxification of these radicals is vital in alleviating the damage caused by Fe^{2+} and is responsible for tissue tolerance (Yamanouchi and Yoshida, 1981; Vose, 1983). Tolerance mechanisms may involve strong binding or incorporation of Fe^{2+} by ferritin into symplast that allows controlled oxidation/reduction reactions (Bienfait, 1985). The extent of ferritin formation has been hypothesized to be a possible protection mechanism against high concentrations of Fe^{2+} in the symplast (Landsberg, 1996). The ferritins, store and buffer iron inside the plastids (Briat et al., 1999) and these proteins are also likely to be present in the mitochondria (Zancani et al., 2004). ROS scavengers such as cytosolic ascorbate (Hu et al., 1999) or glutathione (Thongbai and Goodman, 2000) have also been shown to reduce oxidative stress as induced by Fe^{2+} (Larson, 1988; Thompson and Legge, 1987). Much of the ROS scavenging inside the leaf cell of rice, however, is associated with superoxide dismutase (SOD) isoenzymes. The activity of SOD results in the formation of hydrogen superoxide. While this H_2O_2 is a less reactive oxidizing agent than the radicals, it reduces the activity of SOD (Cakmak, 1988). Hence, to effectively prevent oxidative damage, H_2O_2 needs to be further detoxified by catalases and/or peroxidases (POD) (Gupta et al., 1993). The combined

SOD-POD enzyme activity has been established to be largely responsible for preventing Fe^{2+} induced oxidative stress in rice leaves. This mechanism may be of particular importance in situations of seedling toxicity (poorly developed aerenchyma) and especially when rice plants have been injured during transplanting and are exposed to an uncontrolled influx of Fe^{2+} (Yamauchi and Peng, 1995). The genetic variability of SOD-POD activity in the available gene pool is largely unknown and has not been used as a screening tool by rice breeders (Becker and Asch, 2005).

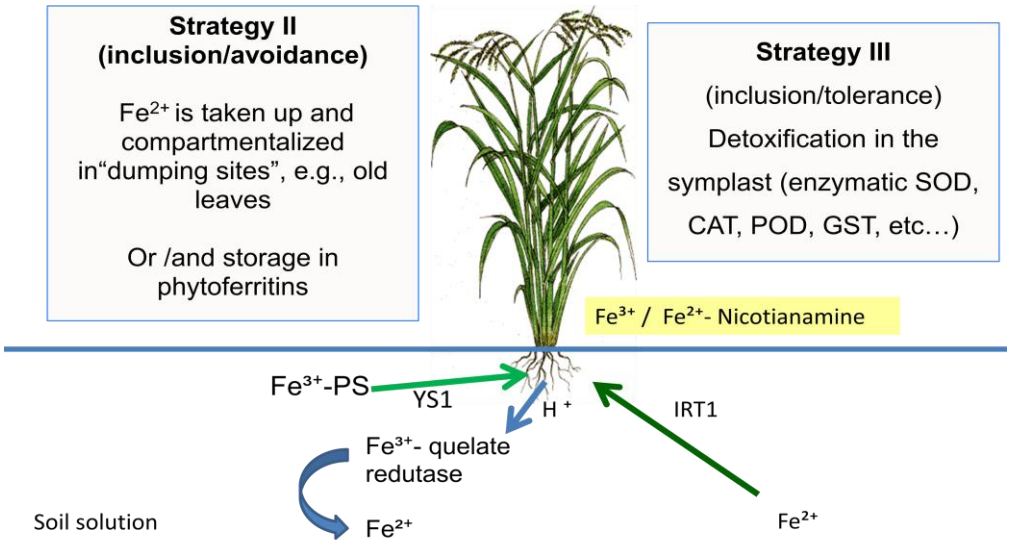

Figure 1.2. Adaptation strategies of rice plants to iron excess in soil. The strategy I is exclude iron at root level. The strategy II exclude Fe^{2+} at the root level and hence avoid of Fe^{2+} damage to the shoot tissue (rhizospheric oxidation and root ion selectivity). The strategy III actually tolerate elevated levels of Fe^{2+} within leaf cells, probably via enzymatic "detoxification" in the symplast. PS (phytosiderophore), YS1 (Yellow stripe 1), IRT (Iron related transporter), SOD (superoxide dismutase), POD (peroxidase), GST (gluthatione S-transferase). Source: Adapted from Becker and Ash (2005).

ROS can be viewed as cellular indicators of stress and as secondary messengers involved in the stress-response signal transduction pathway thus, their level has to be kept under tight control by ROS-scavenging mechanisms, including enzymatic and non-enzymatic antioxidants (Latowski et al., 2010). Under normal growth conditions, the antioxidative defence system provides the adequate protection against reactive oxygen species (Foyer and Halliwell 1976; Fridovich 1986; Asada and Takahashi 1987). However, under abiotic and biotic stresses the balance between ROS production and

scavenging them by antioxidants may be changed and then ROS are generated in excess leading to cell death (Latowski et al., 2010) (Figure 1.3).

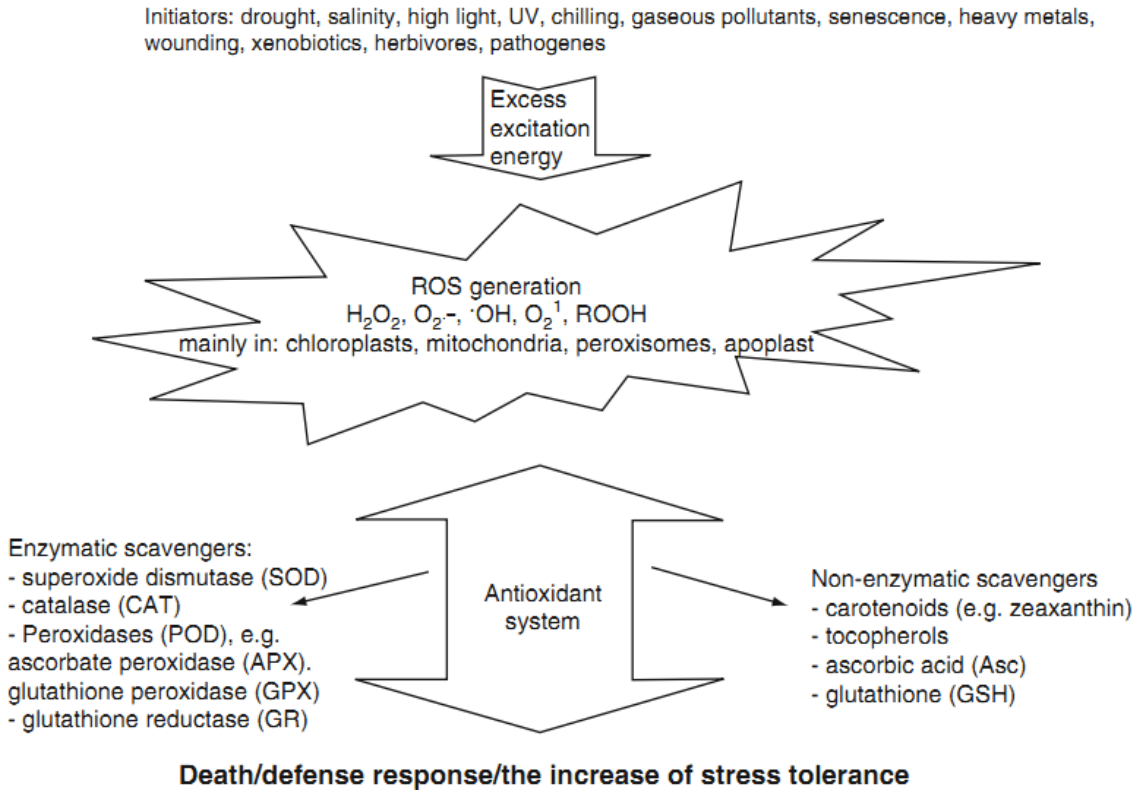

Figure 1.3 The response of plants to different abiotic and biotic stresses. The antioxidant system enables plants to regulate reactive oxygen species (ROS) level and influence on ROS-dependent signal induction. Source: Latowski et al. (2010)

The ROS network signaling can activate both, responsive genes - such as enzymatic antioxidant system - that include the enzymes: superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPOX), glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione S-transferases (GST), glutathione peroxidase (GPX), as well non-enzymatic antioxidant system such as ascorbic acid (Vitamin C), glutathione (GSH), proline (Pro), alpha-tocopherols (Vitamin E), carotenoids (Car) and flavonoids (Figure 1.3).

GSH is present at millimolar concentrations in plant cells and participates in stress resistance and adaptation, such as detoxification of heavy metals and scavenging of ROS generated during normal cell metabolism and induced by biotic and abiotic factors (Noctor and Foyer 1998; Cobbett 2000). However, besides playing critical roles in stress responses,

evidence is currently emerging that GSH is also crucial for many plant developmental processes (Mahmood et al., 2010).

1.5 *Iron Toxicity Symptoms*

The expression of symptom of iron toxicity in rice requires an excessive uptake of ferrous ions (Fe^{2+}) by the roots and their acropetal translocation through xylem outflow to the aerial parts. Inside the leaf, such significant quantities of iron cause increased production of radicals that can irreversibly damage cell structural components (Thompson and Ledge, 1987) and cause an accumulation of polyphenylene oxides (Yamauchi and Peng, 1993). The typical visual symptom linked to this is the "bronzing" or yellowing processes of the rice leaves (Howeler, 1973).

The typical visual symptom connected to the process described above, especially due to the accumulation of polyphenol oxides, is called bronzing or yellowing of rice. Because of the low mobility of iron in the plant, these typical symptoms start with reddish to brown light pitting of older leaves. This pitting then spreads all over the leaf, which bronzes. In later symptom development, leaf tips become yellow-orange then dry up for some rice varieties. These symptoms are particularly developed on the older foliar organs with high transpiration rates (Yamanouchi and Yoshida, 1981). Then the whole leaf becomes orange to brown or purple brown when the toxicity is severe (Fairhurst and Witt, 2002).

These symptoms can occur at different growth stages and can affect rice at the young plant stage, during the whole vegetative growth stage, and in the reproductive stages. According to the growth stage at which they appear, other symptoms and growth effects can occur. In the case of toxicity at the seedling stage, rice plant development stops, and tillering is extremely limited (Abraham and Pandey, 1989).

Toxicity in the vegetative stages causes a reduction in height and dry matter (Abu et al., 1989). The aerial biomass can be more affected than root biomass (Fageria et al., 1988). Tiller formation and the number of productive tillers can be drastically reduced (Cheema et al., 1990).

When iron toxicity occurs at the end of the vegetative stage or at the beginning of the reproductive stage, the number of panicles decrease (Singh et al., 1992), spikelet sterility increases (Virmani, 1977) and the flowering and maturity stages can be delayed by 20-25 days. For some highly sensitive cultivars no flowering takes place (Ayotade, 1979). The

oxidizing ability of the roots decreases and the root surfaces become dark because of precipitates of $Fe(OH)_3$ compounds (Morel and Machado, 1981).

There are strong correlations between the severity of iron toxicity symptoms and yield and it impact on the crop varies according to cropping season and year (Audebert, 2006). Yield losses associated with the occurrence of the symptoms generally range from 15 - 50%. In the case of serious toxicity, however, total harvest loss can occur (Abifarin, 1989; Audebert and Sahrawat, 2000). But when the crop meets iron toxicity at the beginning of the cycle, plant growth can be strongly affected and total yield loss is conceivable (Abifarin, 1988). Seasonal and inter-seasonal variations observed (symptoms and yield) are mainly due to transpiration variations and differences in acropetal translocation of iron in the plant. Iron toxicity effects are more intense in the dry season than the wet season (Sahrawat and Diatta, 1995; Audebert and Sahrawat, 2000).

1.6 *Genetic Signaling Network in Response to Oxidative Stress Caused by Iron Toxicity*

The responses of plants to stress have a complex nature and its perception requires the interaction between multiple sensors. After initial recognition of stress by cells, a signal transduction cascade is triggered through secondary messengers that transmit the signal, activating responsive genes and generating an initial response. The products of the induced genes may be involved in response to stress (i.e. tolerance) and in signal transduction. The stress tolerance genes enable plants to cope with these adverse conditions with responses short and long term responses (Grennan, 2006).

Transcription factors (TFs) regulate the expression of genes at the transcriptional level, thus the changes in the activities of TFs dynamically change the transcriptome, resulting in metabolic and phenotypic changes in response to certain stimuli. TFs regulate the first step of gene expression and are usually defined as proteins containing a DNA-binding domain (DBD) that recognize a specific DNA sequence (Mitsuda and Ohme-Takagi, 2009) this DNA sequences are known as *cis*-regulatory elements located in a promoter region of genes.

Various transcription factors interact with *cis*-regulatory elements in promoter regions and form a transcriptional initiation complex on the TATA box (core promoter) upstream of the transcriptional initiation sites (Figure 1.4).

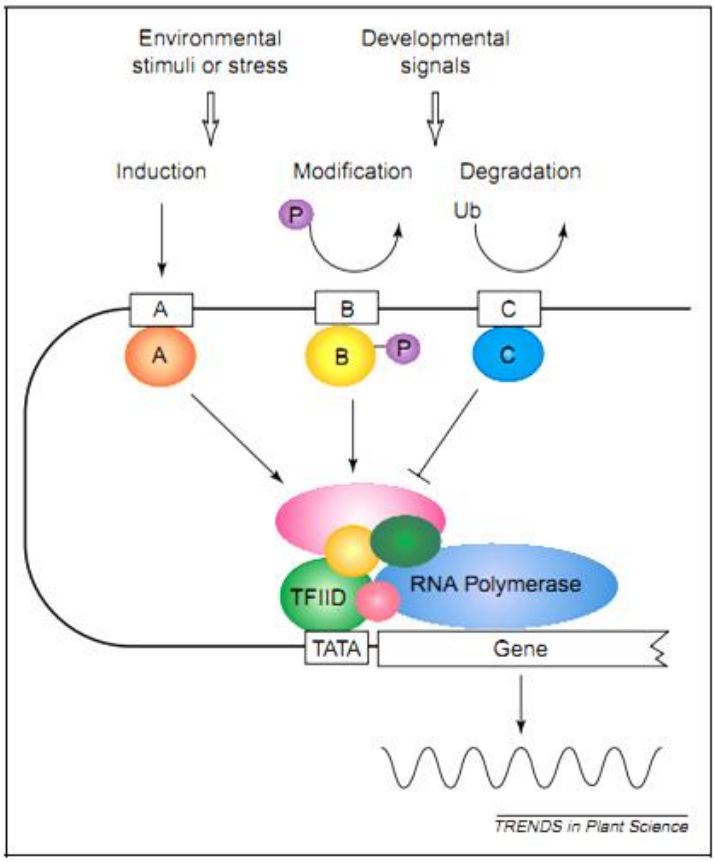

Figure 1.4 Schemes of transcriptional regulatory networks. The transcriptional initiation complex is regulated by transcription factors that are activated or repressed by environmental stimuli and/or developmental signals. The rectangular boxes labeled A, B and C represent the cis-acting factors and the ellipses labeled A, B and C represent the transcription factors. Abbreviation: Ub, ubiquitin. Source: Yamaguchi-Shinozaki and Shinozaki (2004).

The transcriptional initiation complex then activates RNA polymerase to start transcription of stress-responsive genes. In this process, various interactions between *cis*-regulatory elements and transcription factors function as molecular switches for transcription to determine tran-scription initiation events. Abiotic stress signals activate transcription factors by induction of their genes, activation of proteins (such as phosphorylation), and degradation of proteins through the proteasome system (Yamaguchi-Shinozaki and Shinozaki (2004) (Figure 1.4).

Under iron stress conditions a burst of oxidative stress takes place since, in addition to ROS being continuously produced as byproducts of various metabolic pathways that are localized in different cellular compartments such as chloroplast, mitochondria and peroxisomes (del Rio et al., 2006; Navrot et al., 2007) ROS are generated by Fenton and Haber Weiss reactions that increase under iron excess.

ROS affect many cellular functions by damaging nucleic acids, oxidizing proteins, and causing lipid peroxidation (LPO) (Foyer and Noctor, 2005; Gill and Tuteja 2010). The equilibrium between the production and the scavenging of ROS may be perturbed by various biotic and abiotic stress factors such as salinity, UV radiation, drought, heavy metals, extreme temperatures extreme, nutrient deficiency, air pollution, herbicides and pathogen attacks (Gill and Tuteja, 2010). Accumulation of ROS as a result of various environmental stresses is a major cause of loss of crop productivity worldwide (Mittler, 2002).

On the other hand, it is important to note that ROS can act as damaging, protective or signaling factors depending on the delicate equilibrium between ROS production and scavenging at the proper site and time (Gratão et al., 2005; Mittler, 2004). ROS can damage cells as well as initiate responses such as new gene expression. The stimulated cell response is strongly dependent on several factors, for example, the subcellular location for formation of an ROS may be especially important for a highly reactive ROS because it diffuses only a very short distance before reacting with a cellular molecule.

The delicate balance between ROS production and scavenging that allows this duality of function to exist in plants is thought to be orchestrated by a large network of genes termed the 'ROS gene network', which includes more than 152 genes in *Arabidopsis*, tightly regulating ROS production and scavenging (Mittler et al. 2004).

Plant stress tolerance may therefore be improved by the enhancement of *in vivo* levels of antioxidant enzymes (Gill and Tuteja, 2010).

Concerning the iron toxicity, two cellular pathways have been implicated in the differential regulation of various plant ferritin genes: one involves abscisic acid (ABA) (the plant stress hormone) and other is ABA independant, and modulated by antioxidants and serine/threonine phosphatase inhibitors (Briat and Lebrun; 1999, Briat and Lobreaux, 1997; Savtno et al., 1997). Plant ferritins are, therefore, likely to constitute an important component of the oxidative stress response in plants, and probably participate in the protection of plastids against oxidative stress by storing excess free iron. In addition to an increase in ferritin concentration, iron excess also increases the concentration of dehydroascorbate and decreases the ascorbate concentration (Kanpfenkel et al., 1995; Briat and Lebrun, 1999).

Genes responsive to ABA are also expressed in response to iron treatment, this suggests that ABA may be involved in the transduction pathway leading to ferritin

synthesis in response to iron. Iron overload of maize plantlets leads to a fivefold increase in ABA concentrations in roots and leaves, and the abundance of ferritin mRNA increases in response to an exogenous ABA treatment (Briat and Loubréaux, 1997).

For a long time H_2O_2 (a type of ROS) has been considered mainly a harmful oxidant, whose accumulation in response to stresses leads to unspecific oxidation and necrosis. However, now it has been recognized that H_2O_2 also acts as a secondary signalling compound inducing defence pathway including e.g. the MAPK (mitogen activated protein kinase) cascade (Kovtum et al. 2000).

Links with calcium and protein phosphorylation networks have been extensively studied, for example in the case of the ROS generating respiratory burst oxidase (RBOH) NADPH oxidase proteins that contain an EF-calcium binding as well as phosphorylation domain(s) (Kobayashi et al., 2007; Ogasawara et al., 2008). In addition, ROS levels are linked with cellular redox networksthrough thioredoxins, peroxiredoxins, glutaredoxins and/or NADPH (Moon et al., 2004; Rouhier, 2010).

The MAPK cascade is one of the most commonly studied mechanisms in signaling, comprising a class of protein kinases that play a crucial role in eukaryotic systems, often linking perception of external stimuli with changes in cellular organization or gene expression. They play a pivotal role in biotic and abiotic stresses as well as a range of developmental responses including differentiation, proliferation and death (Taj et al., 2010).

A MAPK cascade minimally consists of a MAP3K-MAP2K-MAPK (Figure 1.5) module that is linked in various ligand-binding site configurations of proteins to upstream receptors and downstream targets.

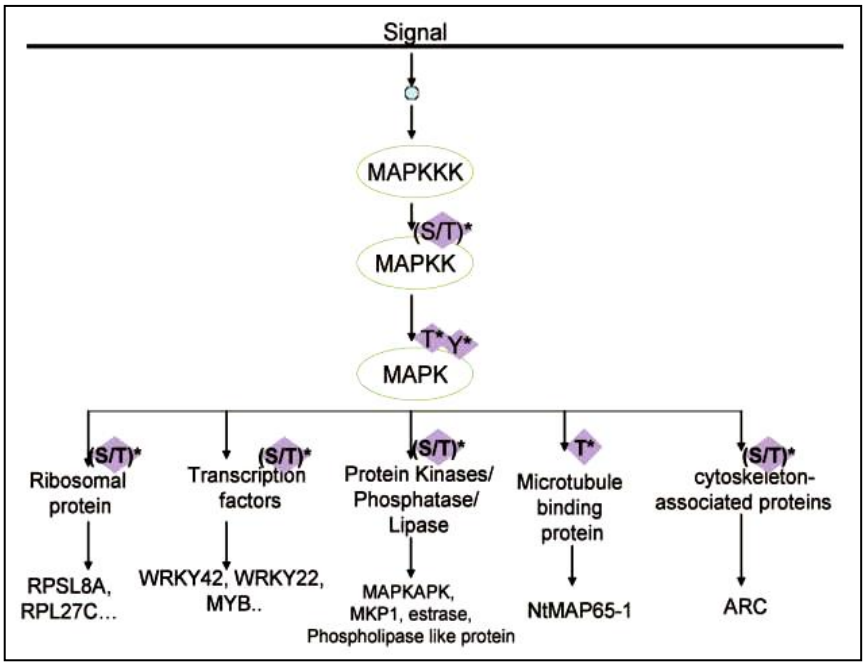

Figure 1.5 A signal transduction cascade navigates the signal from MAPKKKK to MAPK by triggering a series of Threonine (Y)/Tyrosine (T) and Serine (S)/Threonine phosphorylation events, finally culminating in activated MAPK being transported to the nucleus where it is involved in the phosphorylation of transcription factors and reconfiguring a specific response related transcriptional reprogramming. Source: Taj et al. (2010).

Among all components, MAP2Ks act as a point of intersection and integration between converging signals from upstream MAP3Ks and divergent outputs through downstream MAPKs (Menges et al., 2008). Activation of a MAP3K can occur through physical interaction or phosphorylation by the receptor itself, intermediate bridging factors or interlinking MAP4Ks (Swarbreck et al., 2008). MAP3Ks are serine/threonine kinases that activate MAP2Ks through phosphorylation on two serine/threonine residues in a conserved S/T-X3-5 -S/T motif (Nakagami et al., 2005), while MAP2Ks are dual-specificity kinases that phosphorylate MAPKs on threonine and tyrosine residues in the T-X-Y motif (Taj et al., 2010).

Many different MAPK cascades can be activated following ROS accumulation, Mittler et al. (2011) highlight that MAPKKK MEKK1, MPK4 and MPK6 are among the ROS-responsive (Teige et al., 2004; Jammes et al., 2009; Xing et al., 2008). The MEKK1 pathway is highly active during abiotic and oxidative stress conditions, and MEKK1 is an activator of two homologous MAPKKs (MKK1 and MKK2), which function upstream of the MAPKs MPK4 and MPK6 (Figure 1.6).

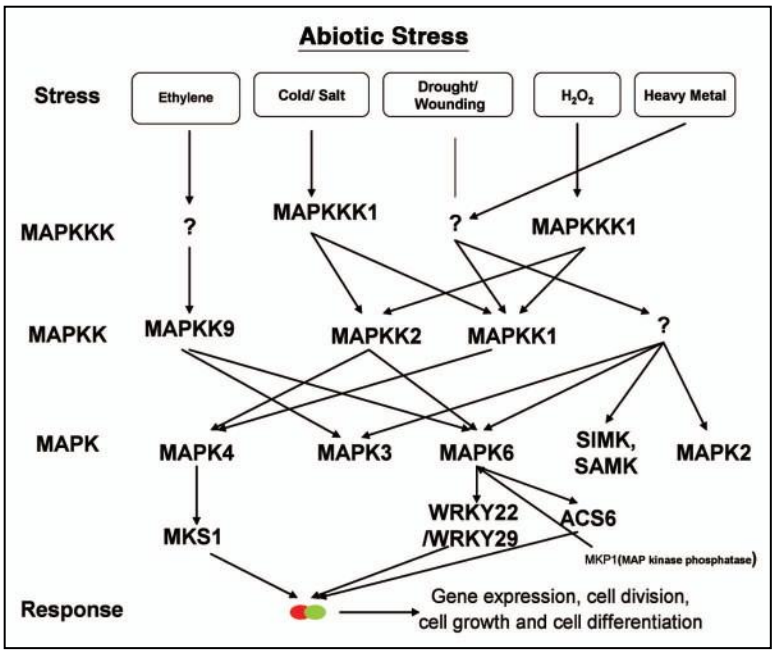

Figure 1.6 Model describing the interconnectivity between different members of kinases cascades involve in abiotic stress responses. Source: Taj et al. (2010).

It has been reported that plant specific WRKY transcription factors that contain the WRKYGQK core sequence and zinc-finger motif are phosphorylated by MAPKs, like MAPK4. This signaling cascade appears to be mediated through interaction with MKS (MAP kinase substrate) and the target WRKY transcription factors such as WRKY25 and WRKY33 (Menke et al., 2004; Andreasson et al. 2005). WRKY transcription factors are associated with MAPK in the nucleus and the majority of terminal MAPKs appear to be within nucleus, associated with transcriptional complexes at target genes (Pokholok et al., 2006).

In rice, in an immunokinase essay in arsenite treated seedling, Rao et al. (2011) verified a significant level of induction in *OsMPK3* transcripts in leaves and *OsMPK3*, *OsMPK4* transcripts in roots. Among MAP2K kinase gene family, *OsMAP2K4* transcripts were found to be induced in arsenite treated rice leaves and roots.

Key components of the reactive oxygen gene network have been identified by reverse genetics. Recent studies with mutant lines of knockout and antisense for *Cat2*, *Apx1*, *chlAOX*, *mitAOX*, *CSD2*, 2-cysteine PrxR and various NADPH oxidases have revealed a strong link between ROS and processes such as growth, development, stomatal responses and biotic and abiotic stress responses (reviewed by Mittler et al., 2004). These finding demonstrate the complex nature of the ROS gene network in plants and its modulation of key biological

processes. Although mutants for all the proteins listed above are viable, demonstrating the redundancy of the ROS network, a clear phenotype is associated with each of the different genes, suggesting that they play a key role in the ROS signaling network of plants.

Downstream signaling events associated with ROS sensing involve Ca_2C and Ca_2C -binding proteins, such as calmodulin (Knight and Knight, 2001; Coelho et al., 2002), the activation of G-proteins (Baxter-Burrell, et al., 2002), and the activation of phospholipid signaling, which results in the accumulation of phosphatidic acid (Anthony et al., 2004; Rentel et al., 2004).

A serine/threonine protein kinase (OXI1) has been shown to play a central role in ROS sensing and the activation of MAPKs 3 and 6 by Ca_2C (Rentel et al., 2004). This kinase is also activated by PDK1 through the phospholipase-C/D-phosphatidic-acid pathway (Anthony et al., 2004). A MAPK cascade involving MAPK3/6 acts downstream of OXI1 and controls the activation of different defense mechanisms in response to ROS stress (Kovtun, et al., 2000; Apel and Hirt, 2004). The expression of different transcription factors is enhanced by ROS and includes members of the WRKY, Zat, RAV, GRAS and Myb families (Mittler et al., 2004). Gene expression analysis reported by Gadjev et al. (2006) shows that of the 32 transcription factors to be highly responsive to multiple ROS-inducing conditions, 20 are regulated by the MEKK1, predominantly via the MEKK1–MKK1/2–MPK4 pathway (Pitzschke et al., 2009) which include WRKY25, WRKY33, WRKY40, zinc finger (CCCH-type), zinc finger (C2H2 type), zinc finger (C_3HC_4-type RING finger), ANAC062, ARABIDOPSIS ZINC-FINGER PROTEIN 2, scarecrow-like transcription factor 13 among others. Studies using knockout in plants have revealed that the zinc-finger protein Zat12 is required for *Apx1* expression and plant protection during oxidative stress (Rizhsky, et al., 2004), and that the highly conserved zinc-finger paralogs LOL1 and LSD1 have antagonistic effects on SOD and O2K accumulation (Epple et al., 2003).

CHAPTER II

TRANSPOSABLE ELEMENT DYNAMICS IN GENOME AND ITS RELATION WITH GENES

2.1 Transposable elements in genome

Transposable elements (TEs) are all mobile DNA segments in the genome, regardless of their mechanism of transposition, TEs were first described by Barbara McClintock (in the 50s). All transposable elements share two basic properties. The first is the ability to move from one place to another in the genome – hence their designation as mobile DNAs or transposable elements. The second is their ability to amplify their copy numbers within the genome via this transposition, thereby providing a selectable function that can make them selfish or parasitic DNAs (Bennetzen, 2000).

TEs are ubiquitous components of eukaryotic genomes and are also powerful agents of evolutionary change. For example, they impact gene expression via the introduction of alternative regulatory elements, exons, and splice junctions (Jurka 1995; Speek 2001; Nigumann et al. 2002; Kazazian 2004; Peaston et al.2004; Matlik et al. 2006; Babushok et al. 2007; Hasler et al. 2007).

The LTR retrotransposons (long terminal repeat retrotransposons) belong to class I and are the main components of most plant genomes (Kumar and Bennetzen, 1999). The rice genome is composed of 40% of TEs, of these 22% are LTR retrotransposons (Ma et al., 2004), and these proportions are even greater in plants with large genomes such as *Zea mays* (~80%) and common wheat (~ 90%) (Mccarthy et al. 2002; Gao et al. 2004; KashKush et al. 2007).

There is, therefore, a powerful selection pressure for TEs that can achieve a balance between their own replication and minimal damage to their host. Epigenetic regulation proves to be a widespread manner to achieve this balance, quieting transposition on the one hand, yet allowing it on the other, when organisms are challenged by adverse environmental circumstances. As our understanding of epigenetics improves, the subtleties and the scope of how TEs can affect gene expression, both directly and indirectly, are becoming clearer (Weil and Martienssen, 2008).

Several rice genes contain TE derived sequences (Sakai et al., 2007). However, TE influence in gene expression is not restricted to physical modification of chromosomes (Vicient, 2010).

Both LTR and non-LTR retrotransposons, as well as DNA TEs, can regulate nearby genes, and this regulation depends on epigenetic mechanisms that silence the elements themselves (Slotkin and Martienssen, 2007).

TEs play an important role in unequal homologous recombination events (Kazazian, 2004). Recent insertion and excision of TEs have given rise to a series of “transposon

insertion polymorphisms" (TIPs; polymorphisms consisting of the presence/absence of a TE at a particular chromosomal location) in closely related species, subspecies, and haplotypes and served as ongoing sources of genomic and genetic variation (Bennett et al., 2004).

One example was observed by Huang et al. (2008) where the insertion of LTR *copia* in the 3´ UTR region of *OsWRKY8* gene created an alternative isoform in Nipponbare, which is a chimeric transcript possessing three additional exons from the TE. *OsWRKY8* is a member of the WRKY gene family encoding transcription factors that are involved in the regulation of various biological processes (Xie et al., 2005). Two alternative transcript isoforms coexist in Nipponbare: one is identical to the gene isoform of indica 93-11, while the other acquired four additional exons in the transposon region, thus giving rise to a chimeric gene containing both a principal part of the host *OsWRKY8* gene and a fraction of the LTR (Huang et al., 2008).

Furthermore, one recent publication provided strong arguments suggesting that increases in transposable element activity in response to physiological stress may provide the foundation for the punctuated equilibrium model of evolutionary change (Zeh et al., 2009).

Studer et al. (2011) verified that a miniature inverted-repeat transposable element (MITE) Hopscotch inserted in a regulatory region of the maize domestication gene, *teosinte branched1* (*tb1*), acts as an enhancer of gene expression and partially explains the increased apical dominance in maize compared to its progenitor teosinte. In addition, these authors found molecular dating indicates that the Hopscotch insertion predates maize domestication by at least 10,000 years, indicating that selection acted on standing variation rather than new mutation.

2.2 Transposable elements classification

TEs are generally classified according to their transposition intermediate and their known or supposed transposition mechanisms, these transpositions occur in *cis* when the element is autonomous and translates its own proteins, or in *trans* when the element is defective, the latter being dependant on coding abilities of the autonomous elements. The transposition intermediate allows these separation of the TEs in two major classes: the Class I elements have a reverse transcribed RNA intermediate, whereas the Class II element have only a DNA intermediate (Sabot et al., 2004).

Class I represent the LTR retrotransposons that replicate using a RNA intermediate, through a "copy-and-paste" mechanism. They are related to retroviruses with which they share their structure: a complete copy consists of two LTRs that flank an internal region. LTR

sequences contain the signals for transcription initiation and termination, while the internal region encodes the proteins that are necessary for the retrotransposition cycle. Both LTR retrotransposons and retroviruses are flanked by LTRs that provide *cis*-regulatory sequences required for transcription of an RNA intermediate (Boeke and Corces, 1989). The internal sequences of these elements encode proteins (GAG, protease, integrase, reverse transcriptase, and RNaseH) necessary for reverse transcription and integration.

Based on the arrangement of their protein-coding domains, LTR retrotransposons are classified into two major families: the *Ty1/copia-like* and *Ty3/gypsy-like* elements (Vitte et al., 2007). The integrase domain is positioned in the 3' region of the reverse transcriptase domain in *gypsy*-like retrotransposons, and in the 5' region of reverse transcriptase in *copia*-like retrotransposons (Figure 2.1).

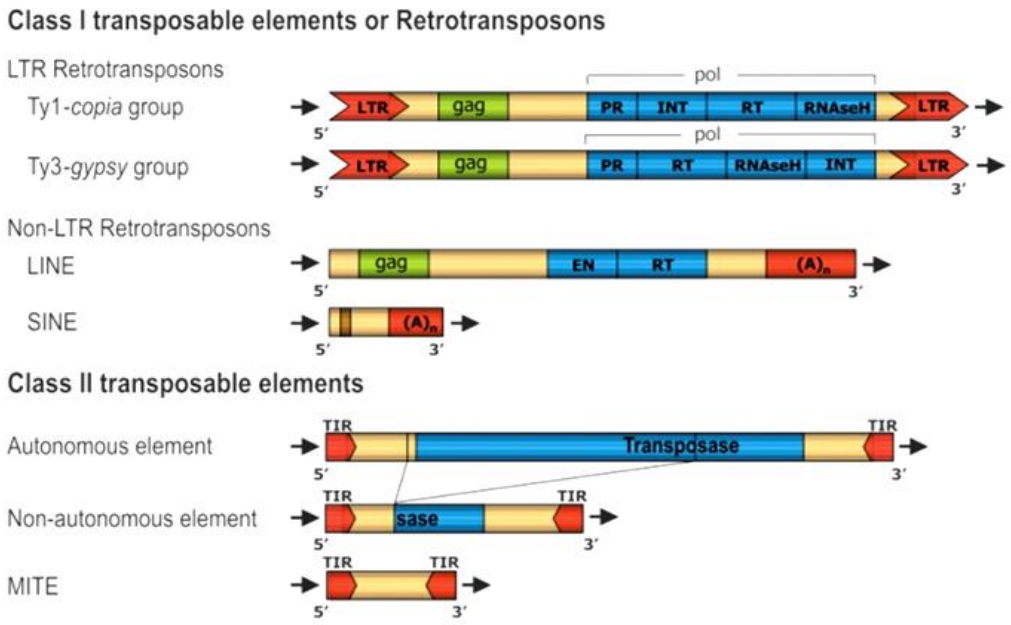

Figure 2.1 Structure of the different types of plant transposable elements. PR (protease), INT (integrase); RT (reverse transcriptase); LTR (long terminam repeat); TIR (terminal inverted repeats); EN (envelope). Source: Casacuberta and Santiago (2003).

Class II elements have a conservative model of transposition "Cut-and-Paste". For all Class II elements, the transposition intermediate is DNA. The DNA sequence moves or duplicates "itself" from the first location (donor site) to another genomic location (acceptor site); in the first two subclasses, the protein responsible for the movements is the transposase. The transposition enzymes could be encoded by the element itself (autonomous element), or by another element ("defective"/non-autonomous element) (Sabot et al., 2004).

Retrotransposons mobilize themselves by the reverse transcription of an RNA intermediate; however, different types of retrotransposons carry out this process by distinct mechanisms. LTR retrotransposons and non-LTR retrotransposons use element-encoded enzymes to mediate their mobility (Figure 2.2). In addition, the endonuclease and reverse transcriptase activities of non-LTR retrotransposons also have a central role in mobilizing non-autonomous short interspersed elements (SINEs) (Kajikawa and Okada,. 2002; Dewannieux et al., 2002; Hancks et al., 2011), certain classes of non-coding RNAs (Garcia-Perez et al., 2007; Gilbert et al., 2005; Buzdin et al., 2002; Weber et al., 2006) and messenger RNAs, the latter of which results in the formation of processed pseudogenes (Wei et al., 2001; Esnault et al., 2000) (reviewed by Levin and Moran, 2011).

TEs are potent mutagenic agents with the potential to produce a wide array of changes in the genomes of their hosts (Kidwell and Lisch, 2000; 2001). The range of 'mutations' induced by TE activity extend from modifications in the size and arrangement of whole genomes to substitutions, deletions, and insertions of a single nucleotide. In addition, they have the ability to increase genome size following transposition (Piégu et al., 2006). TEs induce chromosomal rearrangements such as deletions, duplications, inversions, and reciprocal translocations. This activity provides the potential for small and large scale genome reorganization, amplification, and reduction (Kidwell, 2002).

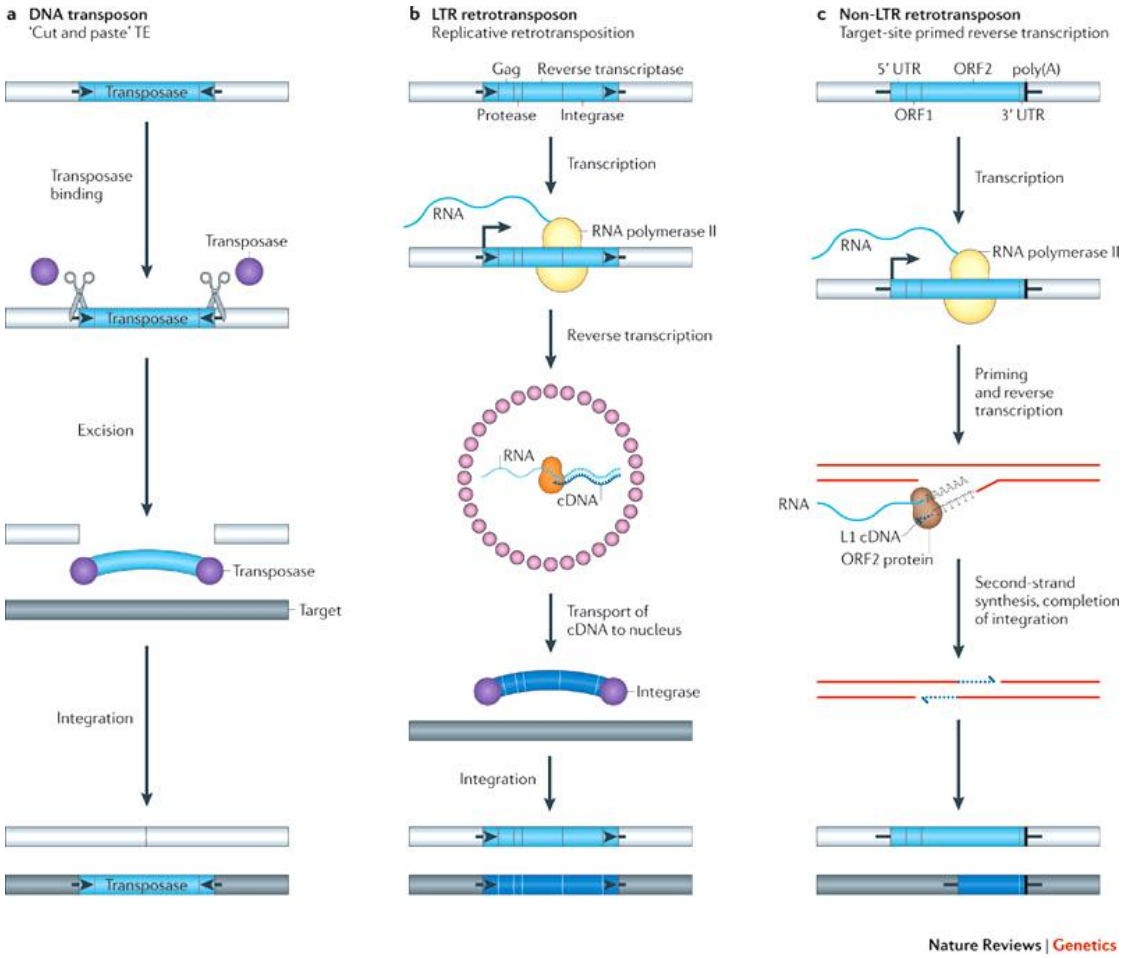

Figure 2.2 The diverse mechanisms of transposon mobilization. a) DNA transposons. Many DNA transposons are flanked by terminal inverted repeats (TIRs; black arrows), encode a transposase (purple circles), and mobilize by a 'cut and paste' mechanism (represented by the scissors). The transposase binds at or near the TIRs, excises the transposon from its existing genomic location (light grey bar) and pastes it into a new genomic location (dark grey bar). The cleavages of the two strands at the target site are staggered, resulting in a target-site duplication (TSD) typically of 4–8 bp (short horizontal black lines flanking the transposable element (TE)) as specified by the transposase. Retrotransposons (b and c) mobilize by replicative mechanisms that require the reverse transcription of an RNA intermediate. b) LTR retrotransposons contain two long terminal repeats (LTRs; black arrows) and encode Gag, protease, reverse transcriptase and integrase activities, all of which are crucial for retrotransposition. The 5′ LTR contains a promoter that is recognized by the host RNA polymerase II and produces the mRNA of the TE (the start-site of transcription is indicated by the right-angled arrow). In the first step of the reaction, Gag proteins (small pink circles) assemble into virus-like particles that contain TE mRNA (light blue), reverse transcriptase (orange shape) and integrase. The reverse transcriptase copies the TE mRNA into a full-length dsDNA. In the second step, integrase (purple circles) inserts the cDNA (shown by the wide, dark blue arc) into the new target site. Similarly to the transposases of DNA transposons, retrotransposon integrases create staggered cuts at the target sites, resulting in TSDs. c) Non-LTR retrotransposons lack LTRs and encode either one or two ORFs. As for LTR retrotransposons, the transcription of non-LTR retrotransposons generates a full-length mRNA (wavy, light blue line). However, these elements mobilize by target-site-primed reverse transcription (TPRT). In this mechanism, an element-encoded endonuclease generates a single-stranded 'nick' in the genomic DNA, liberating a 3′-OH that is used to prime reverse transcription of the RNA. The proteins that are encoded by autonomous non-LTR retrotransposons can also mobilize non-autonomous retrotransposon RNAs, as well as other cellular RNAs (see the main text). The TPRT mechanism of a long interspersed element 1 (L1) is depicted in the figure; the new element (dark blue rectangle) is 5′ truncated and is retrotransposition-defective. Some non-LTR

retrotransposons lack poly(A) tails at their 3′ ends. The integration of non-LTR retrotransposons can lead to TSDs or small deletions at the target site in genomic DNA. For example, L1s are generally flanked by 7–20 bp TSDs. Source: Levin and Moran (2011)

2.3 Transposable elements silencing by host genome

During their evolution, organisms have developed mechanisms to avoid injurious mutations caused by TEs transposition: among the major known mechanisms to silence TEs we can list methylation, control of TE via expression of small RNAs, cytosine deaminases and DNA repair factors which restrict TEs. In the Figure 2.3 is present examples of alterations in phenotype that is associated with tranposon silencing.

DNA methylation is cytosine methylation (to 5-methylcytosine) and is an important DNA modification in eukaryotes (Levin and Moran, 2011). Most cytosine methylation in plants mammals, and in the fungus *Neurospora crassa*, occurs within repetitive elements and is correlated with the transcriptional repression of retrotransposons in somatic and germline cells (Selke et al., 2003; Yoder et al., 1997). Weil and Martienssen (2008) highlighted that appear to be three distinct pathways for silencing the transcription of TEs: one acts through *DDM1* (*DECREASE IN DNA METHYLATION1*), *MET1* (*METHYLTRANSFERASE1*), and *SIL1 (SILENCING1 - histone deacetylase)*, another through a *KYP-CMT3 (KRYPTONITE-CHROMOMETHYLASE 3*) pathway, and the third uses *DRM1 (DDM1: DECREASE IN DNA METHYLATION1)* and *DRM2 (DOMAINS REARRANGED METHYLASE1)* (Lippman et al., 2003; Cao et al., 2003; Kato et al., 2003). At least two of these pathways involve small interfering RNAs, for which transposons are the overwhelming source in plant genomes. Defects in components of each of these systems can reactivate different, sometimes overlapping subclasses of silenced TEs.

Small RNA-based silencing mechanisms include those involving endogenous small interfering RNAs (endo-siRNAs) and *PIWI*-interacting RNAs (piRNAs), which also act to defend eukaryotic cells against TEs. The mechanisms by means of which these small RNAs are generated and how they inhibit is an area of investigation that remains active in various model organisms. Endo-siRNAs have the potential to inhibit TE mobility through the post-transcriptional disruption of transposon mRNA. For example, ‘trigger’ dsRNAs can be derived from: complementation of inverted terminal repeats in DNA transposons, structured mRNA transcripts or overlapping regions contained within convergent transcription units (Sijen and Plasterk, 2003; Ghildiyal and Zamore, 2009; Malone and Hannon, 2009; van Rij and Berezikov, 2009).

The resultant dsRNAs can then be processed into ~21–24 nt endo-siRNAs by members of the Dicer family of proteins (Tabara et al., 199; Malone and Hannon, 2009). These endo-siRNAs are loaded onto an Argonaute protein, and the passing RNA strand (typically in the direction of the TE strand) is degraded. The remaining complex of an ssRNA and Argonaute is called the RNA-induced silencing complex (RISC); the RNA directs RISC to complementary sequences in target mRNAs, leading to their post-transcriptional degradation. In the case of cytosine deaminases and DNA repair factors that restrict TEs, the proteins that are involved in nucleic acid metabolism and/or DNA repair can also restrict TE mobility (Levin and Moran, 2011).

For example, members of the apolipoprotein B mRNA-editing enzyme 3 (APOBEC3) family of cytidine deaminases can restrict the retrotransposition of various retroviruses and LTR and non-LTR retrotransposons (Chiu et al., 2008). For retroviruses and LTR retrotransposons, APOBEC3 proteins generally deaminate cytidines during the first strand cDNA synthesis, which leads to either cDNA degradation or the integration of a mutated provirus (Levin and Moran, 2011).

TEs are a source of regulatory elements, a large body of studies has illustrated the numerous ways by which TEs can directly influence the regulation of nearby gene expression, both at the transcriptional and post-transcriptional levels (Feshotte, 2008). Regardless of whether the regulatory elements arise *de novo* by a few mutations or are pre-existing within TE sequences, the dispersal of expanding TE families throughout genomes potentially allows the same regulatory motif to be recruited at many chromosomal locations, drawing multiple genes into the same regulatory network (Feshotte, 2008).

Additionally, transposases can be a source of DNA-binding domains. As in the case of transcription factors, transposases must translocate to the nucleus to recognize specific DNA sites on the chromosomes. To achieve this, most transposases use a nuclear localization signal and an N-terminal DNA binding domain that interacts specifically with a short DNA motif that is located near each of the transposon ends, often within the TIRs (Craig et al. 2002).

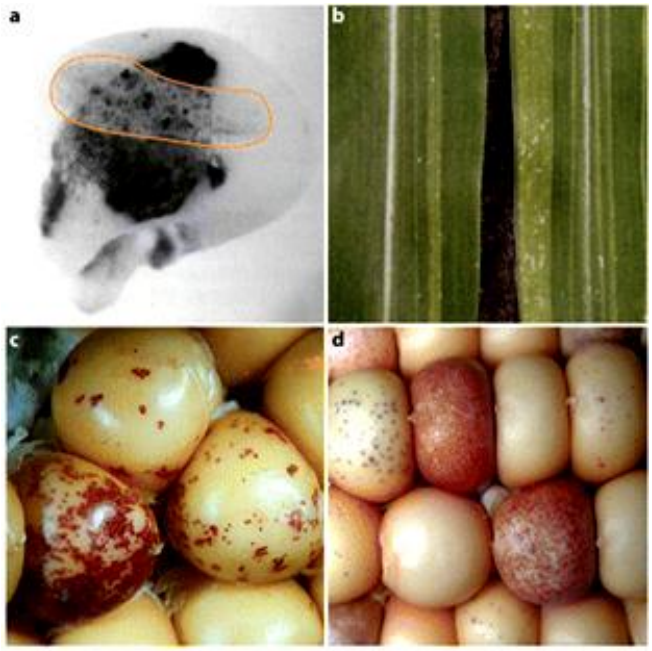

Figure 2.3 Phenotypes associated with transposon silencing in plants. a) Stochastic gain of *Suppressor-mutator* (*Spm*) transposon activity during maize kernel development. Although this kernel inherited an epigenetically silenced *Spm* element, that element reactivated in a clonal sector during development of the kernel. This activity is visualized by observing somatic excisions of a nonautonomous element in a color gene that is expressed on the outer cell layer of the maize seed. A portion of this cell layer was removed (*orange outline*) to reveal the effects of the reactivated *Spm* element on a second responding element, this one inserted in the *waxy* locus. b) Spontaneous silencing of multiple *MuDR* elements in maize as a consequence of inbreeding. Transposon activity is visualized in this case by observing somatic excisions of a nonautonomous reporter element in a color gene. Stochastic variations in silencing result in clonal sectors in which the *MuDR* elements are active or silenced. c) Stochastic loss of *MuDR* activity in a high copy number line. In this case, the expression of two different *Mu*-induced mutations depends on the activity of the *MuDR* elements present. When the elements are silenced, the leaves appear wild type. When the elements are active, two distinct mutant phenotypes are visible: lesion mimicry and chlorophyll depletion. Note that in these plants, as in the kernels in *b*, transposon activity is stochastically lost in somatic clonal sectors. These sectors of lost activity become progressively larger as plant development proceeds. d) Directed genetic loss of *MuDR* activity due to the activity of *Mu killer* (*Muk*). In this case, a family of kernels is segregating for a single *MuDR* element and *Muk*. Plants that inherit both *Muk* and *MuDR* exhibit a uniformly reduced frequency of excision. In subsequent generations, even when *Muk* is lost due to genetic segregation, *MuDR* remains inactive. Source: Lisch (2009).

Also, as in the case of other DNA binding proteins, transposases must either promote their own access to open chromatin, for example, by recruiting host chromatin remodelling complexes (Makarova et al., 2002), or take advantage of a transient relaxation of chromatin at certain regions of the genome (Ros and Kunze, 2001).

In plants, it was reported that the transcription factors Myb-like (helix-turn-helix - HTH), ceNPB (helix-turn-helix - HTH), WRKY (also known as GcM1) (ZF, Zinc Finger), and BeD (ZF – Zinc Finger) are DNA binding domain families probably originated from transposases (Lin et al., 2007).

The evolution of complex multicellular organisms in several branches of the tree of life was accompanied, and perhaps facilitated, by an expansion and diversification of transcription factors. It is thought that the emergence of new transcription factors allowed for the elaboration of increasingly complex networks of genes wired by *cis*-elements that are recognized by different sets of transcription factors (Wilkins, 2002; Davidson, 2006; Levine, 2003).

DNA binding domains derived of transposases are structurally diverse and many can be allied to those that are found in established families of transcription factors, but originally it was often unclear whether the host's DNA binding domains derived from the transposase or vice versa (for example, see Feschotte, 2008), with the accumulation of genomic sequence and the mining of diverse transposons along the eukaryotic tree, it is becoming increasingly clear that these DNA binding domains first originated in transposases (Feschotte, 2008).

2.4 Epigenetics Modifications, Stress and Interplay Between Genes and Transposable Elements

Epigenetics, as originally coined by Conrad Waddington in 1942, referred to the intermediate factor between genotype and phenotype (Waddington and Kacser 1957). Today epigenetics refers mainly to the heritable changes that do not relate to the DNA sequence but can be reliably inherited from one generation to the next. Have been found several mechanisms for epigenetic inheritance have been found, such as DNA methylation, histone modifications, siRNAs, paramutation, nucleosome arrangement, and others. However, the definition of epigenetics is still being debated by biologists and epigeneticists (Bird 2007; Chen et al., 2010).

One important effect of epigenetic regulation is to restrict the transcription of TEs and thus prevent their movement (Mirouze and Paszkowski, 2011). Global analysis in plants such as Arabidopsis and rice suggests that the vast majority of transposons are inactive, methylated, and targeted by siRNAs (Kasschau et al., 2007; Nobuta et al., 2007; Zilberman et al., 2007; Lister et al., 2008). Most TEs are transpositionally inactive, they can be activated by stress (McClintock, 1984) but the condition most often associated with transposon activation in plants is tissue culture, long known to be a source of epigenetic variation (Kaeppler et al., 2000). Some studies have demonstrated the existence of TEs transpositionally active in rice, for example, *Tos 17*, identified by Hirochika et al. (1996), the LINE (Long Interspersed

Nuclear Elements) Karma (Komatsu et al. 2003), *dTok* (Moon et al., 2006), *nDart* (Tsugane et al., 2006), mPing/Pong (Jiang et al. 2003) and recently Lullaby (Picault et al., 2009).

The transpositional activation of the LTR retrotransposon can significantly alter the expression of a gene, which may lead to gene silencing, and transcriptional activation of LTR retrotransposons can alter the expression of adjacent genes. The genomic distribution of TEs has been widely studied in completely sequenced genomes in order to investigate its relationship with the host genes (Minervini et al., 2009). These studies revealed that most elements are in non-coding regions, intergenic sequences and introns (Griffiths et al., 1999), or in large genomic regions poor in genes (as regions of heterochromatin) (Pimpinella et al., 1995). Moreover it was reported that the insertion of TEs near genes may influence its expression (Desset and Vaury, 2005). This influence is significantly associated with the position, and is due to interference in the networks of gene regulation (promoters and enhancers), or due to the introduction of new regulatory elements carried by the TE. The *Gypsy* TEs class in particular are known to affect the expression of nearby genes by specialized sequences that harbor (Melnikova et al, 2002; Gause et al., 2001) (see Figures 2.4 and 2.5).

In wheat, it was shown by Kashkush et al. (2003) that on activation of both Wis 2-1A long terminal repeats drive the readout synthesis of new transcripts from adjacent sequences including the antisense or sense strands of known genes being that activation of these antisense or sense transcripts is associated with silencing or activation of the corresponding genes, respectively.

In Solanaceae, biotic and abiotic agents are known to reverse transposon silencing. The best-studied examples of this phenomenon involve induction of expression of the retrotransposons *Tnt1*and *Tto* (Lish 2009). These elements can be activated by a variety of agents, including extracts from fungi and bacteria, as well as infection, wounding, and a number of abiotic factors (Grandbastien et al., 1997; Grandbastien et al., 2005; Takeda et al., 1999). *Tto1* carries a 13-bp motif that is sufficient to condition responsiveness to tissue culture, jasmonate, biotic elicitors, and wounding (Takeda et al., 1999), and this motif binds to and is regulated by a MYB-related protein, *Nt*MYB2 (Sugimoto et al., 2000). The specific relationship between reactivation and silencing remains poorly understood. siRNAs and DNA methylation are known to be associated with inactive *Tnt1*elements (Andika et al., 2006), but it is not known whether some or all methylation is reversed when the element is reactivated (Lish et al., 2009).

These data, together with the abundance of retrotransposons in genomes and their ability to be activated by various signals, support the view of transposons as potential controlling elements of gene expression (Kashkush et al., 2003)

McClintock (1984) first suggested that TEs were activated in response to challenges to the genome and, since then, the unchaining of the epigenetic silencing of TEs has been described in response to UV exposure, temperature, radiation, wounding, cell culture, pathogen infection and polyploidization (Capy et al., 2000). Stress reactivated TEs might generate the crude diversity that a species requires over evolutionary time to survive the specific stress. This adaptive response is a long-term strategy to increase variability for selection, but might not necessarily need to be genetic, as TE-induced epialleles would also be affected if the control of TEs were lost (Figure 2.4).

The response of TEs to stress can occur through two mechanisms (reviewed in Capy et al., 2000). First, the stress could directly activate TEs and their mutagenic activity. For example, the *Tnt1* retrotransposon in tobacco is reactivated by infection, a process that is mediated through the *Tnt1* LTR promoter, which has regions that are similar to pathogen defense genes that respond the stress-response hormone salicylic acid. Likewise, some TEs in *Drosophila melanogaster* that respond to heat stress also contain the same regulatory motifs as heat-shock inducible promoters. Second, stress might inhibit gene-silencing mechanisms in the genome, indirectly resulting in the reactivation of TEs. For example, position effect variegation (PEV) is temperature sensitive in fission yeast (Allshire et al., 1994) as well as in *D. melanogaster*, as are P element cytotype and hybrid dysgenesis (Kidwell. 1977). Additionally, in *Drosophila simulans*, temperature influences the rate of transposition and, in wild populations, changes in copy number follow a minimum temperature decline (Vieira et al., 1998).

In *Schizosaccaromyces pombe*, the genes and TEs that are activated in abiotic stress conditions are similar to those that are reactivated in histone deacetylation mutants (Hansesn et al., 2005), and stress-response factors cooperate with RNAi in heterochromatic silencing (Jia et al., 2004). These examples demonstrate how the environment can influence the epigenetic regulation of TEs. Once reactivated, these elements can then further alter the genome randomly in response to stress. In one final striking example, dietary supplementation with methyl-group donors for DNA and histone methylation was shown to cause a shift in coat colour in the offspring of *Avy* mice (Wolff et al., 1998).

Mice that had supplemented diets had a statistically significant shift in the colour of their offspring coats compared with non-supplemented control mice. The supplementation

altered the level of DNA methylation of the IAP LTR at the *Avy* locus. Genome-wide, it is not known to what extent diet and other aspects of the environment effect an epigenetic gene expression that is mediated through TEs, and this remains an important question to be resolved (Slotkin and Martienssen, 2007).

In the model plant *A. thaliana*, the overarching effect of TE methylation is to silence transposition (Zhang 2008) as evidenced by significantly increased levels of TE transcription in *met1* methylation mutants (Zilberman et al. 2007; Lister et al. 2008). In addition to preventing proliferation of new TE sequences, silencing of TEs near genes may also prevent the production of aberrant transcripts via read-through transcription beyond terminal TE (Barkan and Martienssen 1991). However, methylated sequences may also affect the expression of nearby genes, typically reducing expression (Jahner and Jaenisch 1985; Lippman et al. 2004; Zhang et al. 2008). On occasion, the reduction of gene expression could prove adaptive. For example, Lippman et al. (2004) demonstrated that expression of the flowering time gene *FWA* is correlated with the methylation status of a nearby SINE-like TE. More generally, however, an alteration of gene expression might be expected due to methylation of nearby TEs and may have deleterious effects on gene and genome function (Hollister and Gaut, 2009).

Gene regulation is often driven by DNA-binding TFs, which are transiently expressed in response to environmental or developmental cues (Martinez and Walhout, 2009). During transcription activation, these TFs act by recruiting general TFs (GTFs) and the RNAPII machinery to their targets. To do this they need to alter the physical barrier formed by chromatin by recruiting chromatin modifiers. During transcription repression, TFs again affect the chromatin environment, but in this case by modifying it in order to impede the RNAPII accessibility. Many studies using epiregulatory plant mutants have reported correlacion between changes in the epigenetic landscapes and transcriptome alteration (Lauria and Rossi, 2011).

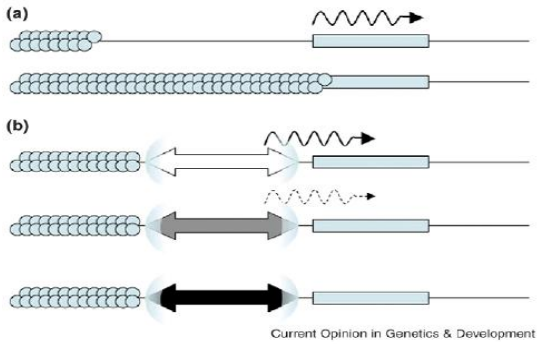

Figure 2.4 - Transposons and spreading. a) Chromatin modifications can influence gene expression, for example by spreading, or signaling from a nearby regulatory region on the same chromosome. b) Transposons (double arrows) can insulate genes from such regions, while simultaneously recruiting epigenetic modifications that bring the gene under their control (grey, black). Co-transcription of the gene and transposon is one mechanism by which genes can come under this control. Source: Weil and Martienssen (2008).

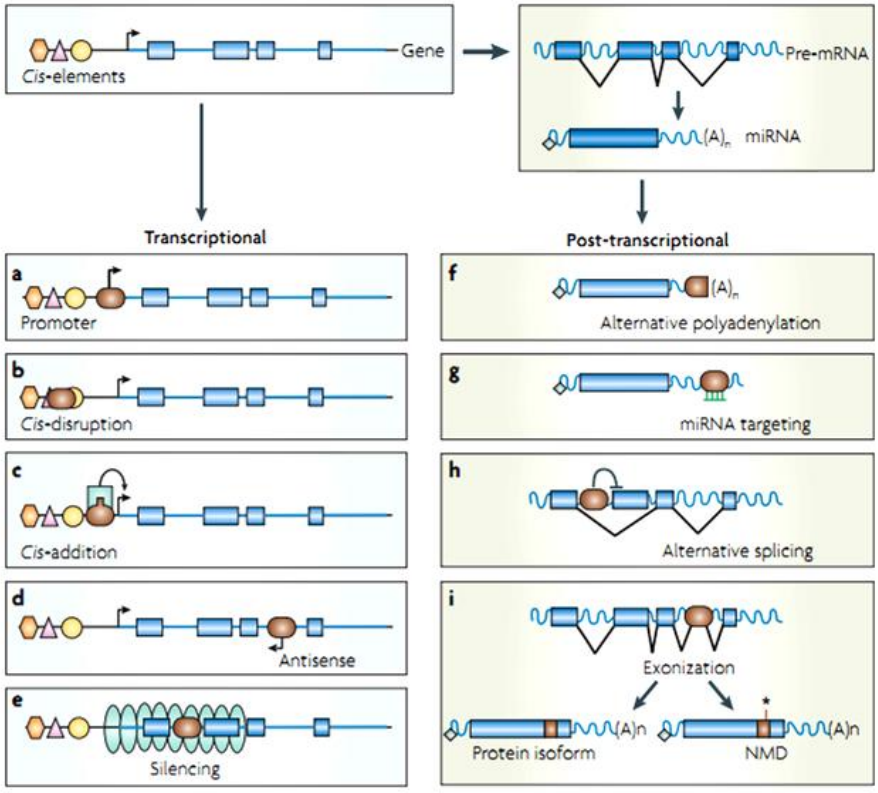

Figure 2.5 Transposable elements can influence gene expression in many ways. At the transcriptional level, a transposable element (TE) (shown in brown) that has inserted upstream of a gene can insert promoter sequences and introduce an alternative transcription start site (a), disrupt existing *cis*-regulatory element or elements (b), or introduce a new *cis* element such as a transcription factor binding site (c). In addition, a TE that has inserted within an intron can drive antisense transcription and potentially interfere with sense transcription (d). Finally, a TE can serve as a nucleation centre for the formation of heterochromatin (green ovals), potentially silencing the transcription of an adjacent gene or genes (e). At the post-transcriptional level, a TE that has inserted in the 3′ UTR of a gene can introduce an alternative polyadenylation site (f), a binding site for a microRNA (g) or for an RNA-binding protein (not shown). A TE that has inserted within an intron can

interfere with the normal splicing pattern of a pre-mrNA (h), provoking various forms of alternative splicing (for example, intron retention and exon skipping). A TE that has inserted within an intron and contains cryptic splice sites can be incorporated (exonized) as an alternative exon (i). This can result in the translation of a new protein isoform, or in the destabilization or degradation of the mRNA by the nonsense-mediated decay (NMD) pathway, especially if the exonized TE introduces a premature stop codon (represented by an asterisk) Source: Feschotte (2008).

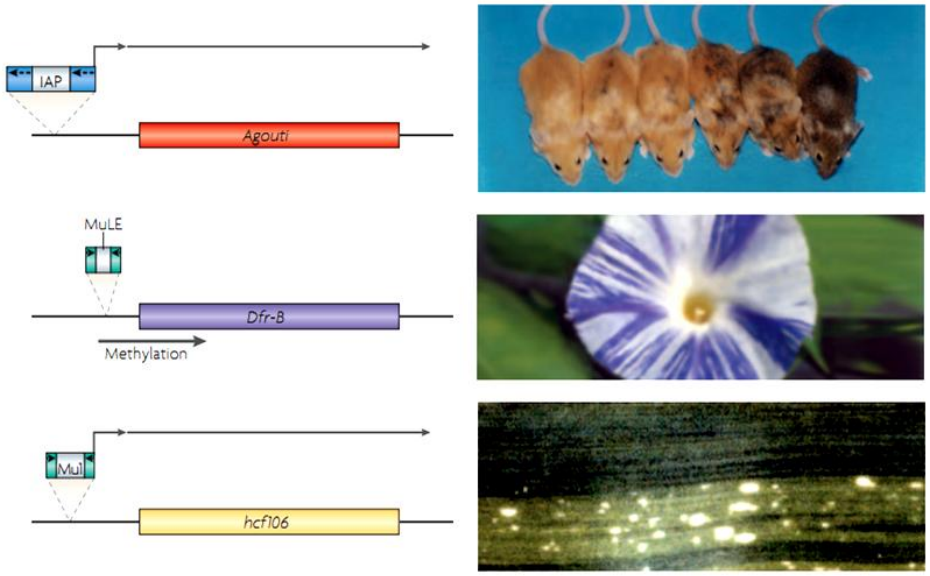

Figure 2.6 Three examples of variegation induced by TE-generated epialleles. In mice, the intracisternal A-particle (IAP) retrotransposon produces an outward-reading transcript that extends into the agouti coat-colour gene. The level of agouti transcript, and the colour of the coat, is subject to the epigenetic status of the retrotransposon and is heritable (Morgan et al., 1999). In morning glory flowers, DNA methylation of a non-autonomous MuLE transposon can spread to the promoter of a flower-colour gene (*Dfr-B*), creating petal-colour streaks (Iida et al., 2004). In maize, the activity of one TE family regulates two epialleles. In sectors where the *Mutator* transposon family is active, the mutant phenotypes of both epialleles occur, generating single sectors of pale green (*hcf106* mutant) and necrotic spotted (*les28* mutant) tissue on leaves (Martienssen and Baron 1994). *hcf106* transcripts are initiated by a non-autonomous (Mu1) transposon only when the autonomous transposon elsewhere in the genome is inactive. Source: Adaptated from Slotkin and Martienssen (2007).

CHAPTER III

MATERIAL AND METHODS

3.1 Plant Material

The experiment was conducted at the Plant Genomics and Breeding Laboratory, at Federal University of Pelotas, Brazil. Pre-germinate seedlings of rice (cv. Nipponbare) with ca. 1 cm of rootlet were transferred to pots containing a complete nutrient solution as described by Camargo and Oliveira (1981): 4 µM $Ca(NO3)_2$; 2 µM $MgSO_4$; 4 µM KNO_3; 0.435 µM $(NH4)_2SO_4$; 0.5 µM KH_2PO_4; 2 µM $MnSO_4$; 0.3 µM $CuSO_4$; 0.8 µM $ZnSO_4$; 30 µM NaCl; 10 µM Fe-EDTA; 0.10 µM Na_2MoSO_4; 10 µM H_3BO_3 and were grown in these conditions for 14 days. The nutrient solution was changed every week, pH was adjusted for 5.5. Subsequent, for iron excess treatment, the plants were transferred to pots containing nutrient solution added with 7 mM of ferrous sulphate ($FeSO_47H_2O$) + EDTA, with pH 4.5 during four days. Control treatment plants were also changed on the 14th day to a complete nutrient solution with pH 4.5. The experiment consisted of three replicates in a completely random design, each replicate consisting of 100 seedlings. During the experiment the photoperiod was 16 hours and photon flux density of 25 µmol $m^{-2}s^{-1}$. On the 18th day, the leaves were collected and stored at -80 °C until extraction of total RNA.

Figure 3.1. Seedlings of rice in nutritive solution. a) 10-day-old without iron excess. b) Leaves of rice (*Oryza sativa* L. ssp. *japonica* cv. Nipponbare) after 18 days of development in a nutrient solution (control treatment). c) Leaves of 18-day-old rice seedlings after four days of iron excess exposure (nutritive solution added from 7 mM of ferrous sulphate ($FeSO_47H_2O$) + EDTA).

3.2 *RNA Extraction, cDNA Synthesis and Hybridizations*

The extraction of total RNA was conducted according to the protocol extraction TRIzol™ Reagent (Invitrogen) and purified with the RNeasy kit (Qiagen). The quality of RNA was verified by agarose gel and then RNAs were assayed by spectrophotometry at an absorbance of 260 nm. The cDNA synthesis was performed according to the protocol Synthesis of Double-Stranded cDNA (NimbleGen) using the SuperScript™ Double-Stranded cDNA Synthesis Kit (Invitrogen). Subsequently, the quality and quantity of double-stranded cDNA were measured by spectrophotometry. To perform the hybridizations the minimum UV

absorbance ratio must be greater than 1.7 at A260nm/A280nm and greater than 1.5 at A260nm/A230nm.

Six hybridizations were peformed, three biological replicates of samples that grew in control condition (nutritive solution with iron content 10 µM Fe-EDTA) and three biological replicates of samples that grew under iron excess cultivation (nutritive solution with 7 mM of ferrous sulphate). The hybridizations were performed with cDNA labeled with cyanine dye (cy3) by Roche NimbleGen™ according with NimbleGen Arrays User's Guide - Gene Expression Arrays 3.1 (2008). After hybridization, the raw data of signal intensity generated for each spot were received. Subsequently, these data were verified, normalized and compared in order to verfy the differential expression. Each one of these procedures will be explained in the next sections.

3.3 *Microarray Design*

The oligo microarray has been produced by NimbleGen™ and is composed of about 385,000 60mers probes selected for their GC content, Tm and number of cycles needed to synthesize the oligo. This chip contains 90,000 probes representing 45,000 genes (2 probes per gene) of rice *Oryza sativa* ssp. *japonica*, 290,000 probes representing all copies of LTR retrotranposons and 1,000 bp of their flanking regions at the 3' and 5' side. The oligonucleotides have been designed at the 3' end of the genes to detect the readings of reverse transcriptase. On the other hand, the retrotransposons are represented throughout their length at the rate of an oligonucleotide at every 500 bp (Figure 3.2).

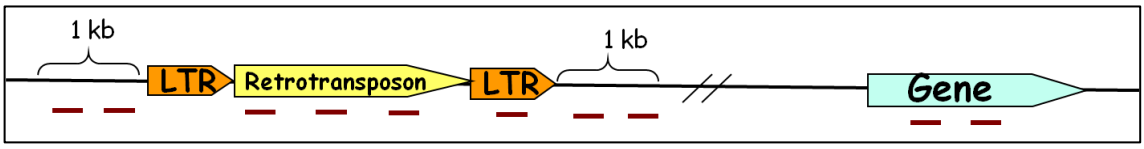

Figure 3.2 Schematic representation of microarray design, red dashes indicate the 60-mer oligonucleotides designed in flanking regions (1kbp up and downstream of LTR retrotransposons) and in each gene of rice (*Oryza sativa* ssp. *japonica*) according to TIGR version 3.

When it was possible, the oligonucleotides have been designed to be unique in the genome (*i.e* locus specific) so as to overcome the problems of oligonucleotides redundancy on the chip. When there were three mismatches during hybridization between a cDNA and an oligonucleotide, the hybridization was considered stable enough to withstand the conditions of washing after the chip hybridization. The oligonucleotides are therefore regarded as locus

specific when they are not matching elsewhere, but having at most three mismatches, which represents 5% of all oligonucleotides.

3.4 *Data Verification*

The data verification is essential because the use of biased data generates erroneous results. The verification is performed by comparing the average, standard deviation and quantiles of each sample, in order to highlight the samples which present excessively different contributions. This verification was done with R statistical software (R Development Core Team, 2006) using the boxplot and summary command. This has enabled us to identify any sample with inappropriate hybridizations.

3.5 *Spatial Effect Correction and Normalization*

Once verified, the data must be normalized in order to be comparable. The first step consists in reducing the space bias effect for each hybridization. Space biases are due mainly to poor washing after hybridization, or a misallocation of signal, manisfested by a gradient of intensity. These biases are corrected by the script SpatialSmooth of NMPP software (NimbleGen Microarray Data Processing Pipeline) (Wang and He, 2006) through a global distance-weighted somoothing algorithm (Figure 3.2).

The second step is to perform the quantile normalization that is the process of adjusting values in a microarray experiment to improve consistency and reduce technical biases and variations between hybridizations. The normalization between hybridizations was performed with the QuantileNorm script of NMPP software. This normalization uses the quantile method which allows a robust normalization between hybridizations of biological repetitions, followed by a global normalization between hybridizations and biological replicates, and then a global normalization was performed between hybridizations of different conditions. Quantile normalizations force the arrays of a set of experiments to have absolutely identical distribution. It is based on the assumption that the RNA populations hybridized to the arrays should be the same. The global normalization adjusts each condition to a same baseline (the median) in order to allow the hybridizations of the different conditions be comparable.

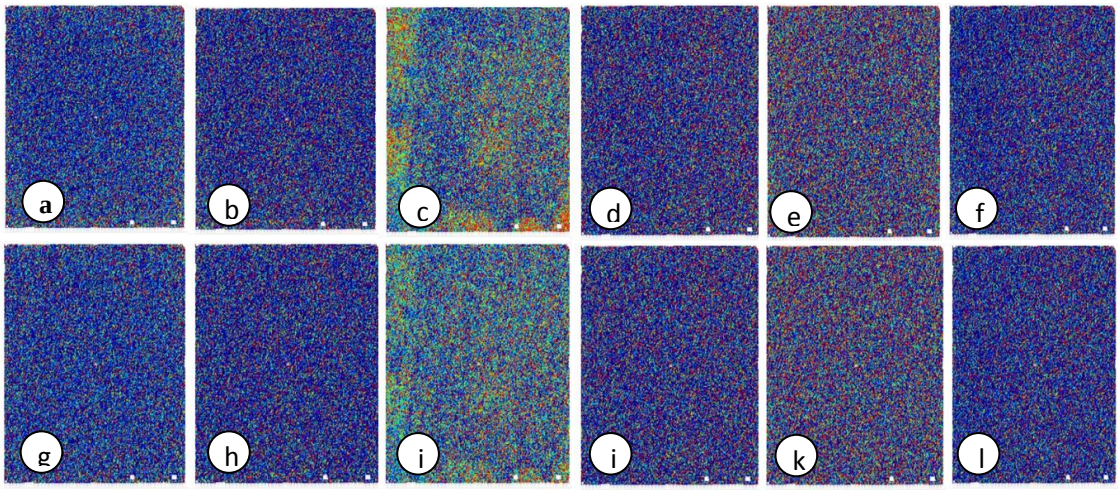

Figure 3.3. Representation of the spots after hybridization with the probe and after correction of spatial effects using SpatialSmooth. a - l) raw intensity values. (a-c) represents the three repetitions of the control condition. (d-f) raw data intensity f the three repetitions of the stress condition of iron – 7 mM). (g-i) intensity values after correction of spatial effects in the control condition. (j-l) intensity values after correction of the spatial effects of stress on the condition of iron excess.

3.6 *Differential Expression Analysis*

To highlight the significant intensity differences of each spot between the two conditions, Limma library (Smyth, 2005) of the Bioconductor package of the statistical software R was used. This script uses a Bayesian T test to determine significant hybridization differences, dismissing the maximum of false positives with BH adjustment (Benjamini and Hochberg, 1995). The package Limma requires the use of Log_2 data and gives the results of different treatment comparison in Log_2-fold change. Traditionally, the oligonucleotides selected are those which present a two fold increase or decrease in expression, i.e, a log-fold change smaller or equal to -1 for underexpression, and greater or equal to 1, for over-expression. In this case all the oligonucleotides displaying p-value ≤ 0.05 for the statistical test were selected.

3.7 *Oligonucleotide Annotation and Gene Ontology*

A local alignment (BLAST) (Altschul et al., 1990) for all oligonucleotides differentially expressed on the chip by considering a log_2-fold-change ≥ 1 and ≤ -1 was achieved using the database RAP-DB (Rice Annotation Project Database - build 5) by considering e-value of 10^{-26} and 57 minimal identity of 60 bp oligonucleotide. This alignment was done because the chip was completed in 2006, the annotations of MSU / TIGR (Rice Genome Annotation), but currently, the database most appropriate and updated for *Oryza sativa* ssp. *japonica* is the RAP-DB. The gene ontology and metabolic pathways was performed using the software Blast2GO (Conesa, et al., 2005) with Gene Ontology

(Ashburner et al., 2000) and KEGG (Kyoto Encyclopedia of Genes and Genomes) (Kanehisa et al. 2011) databases respectively. The Venn diagrams was performed with Venny tool (Olivieros, 2007).

3.8 *Experimental Validation of Microarray by RT-qPCR*

The chip validation was performed by RT-qPCR (reverse transcriptase quantitative PCR) using primers pairs for 15 up-regulated and five for down-regulated genes. The primers design was performed in Primer Express® software (Applied Biosystems, California, United States). Total RNA was digested with DNase I™. The RNA quality was checked by agarosis gel electrophoresis and the RNA quantity was checked in spectrophotometer by measuring the absorbance at 260 nm. The synthesis of cDNA first-strand was performed with SuperScript™ First-Strand Synthesis System for RT-PCR (Invitrogen) from 2µg of RNA. RT-qPCR was performed in Applied Biosystems 7500 Fast Real-Time PCR System using SYBR Green detection system (Applied Biosystems, California, United States). The ΔΔCt relative quantification method (Livak and Schmittgen, 2001) in which the expression data of the target gene were normalized with level of expression of GAPDH (Glyceraldehyde 3-phosphate dehydrogenase) as reference gene, three technical replicates were utilized. The RT-qPCR experiment was performed according MIQE guidelines (Bustin et al. 2009). The amplification was done with Taq Platinum (Invitrogen) with the following program: 50 ºC for 30s, 95 ºC for 10s; 40 cycles of 95 ºC for 30s, 60 ºC for 1 min, and 72ºC for 1 min and a final elongation at 72ºC for 5 min. Pearson's correlation and Mantel Test was performed between the data obtained by microarray and RT-qPCR for each gene validated using Genes Software 7.0 (Cruz, 2006).

3.9 Quantification of Micronutrients in the Tissue of Rice Shoots

The content of micronutrients such as copper (Cu), zinc (Zn), manganese (Mn) and iron (Fe) was determined according to the methodology described by Tedesco et al. (1995) using three replicates of each condition as described in 3.1 item. The data obtained in atomic absorption spectrometry (Thermo Scientific) were calculated based in standard curve for each element. The normality of data was checked and ANOVA F-test was performed in software Winstat 2.0 (Machado and Conceição, 2003).

3.10 cis-Regulatory Elements Pattern Search in Promoters of Up-Regulated Genes

The promoters (1.0 Kbp upstream portions of transcription start site) of up-regulated genes (1,569 genes considering $\log_2 FC \geq 1$) were obtained in RAP-DB database. PLACE – a database of plant *cis*-acting regulatory DNA elements (Higo et al., 1999) was employed to search for information (ID, concensus sequences, TFs related) about reported *cis*-acting regulatory elements (CREs). A Z score for the occurrences for each one of 469 CREs in the 1,569 promoter of up-regulated genes was calculated in order to verify if the probability of the results found was not random. Thus, a cutoff of 0,05 (or 5%) was used to eliminate false positives (Rombauts et al., 2003). The significant occurrences of CREs in gene's promoters were separated in two groups: the group of complex regulation was considered when the CRE occurrence is greater or equal than the average of occurrence in all genes plus two standard deviations; and the group of simple regulation was considered when the CREs occurrences is smaller or equal to the average of occurrence in all genes minus two standard deviations. They were performed a gene annotation and gene ontology using Blast2GO (Conesa et al., 2006) software for each gene group.

Regarding the number of promoter genes where each CRE is significantly present, the CREs with an occurrence equal or greater than average plus two standard deviations were used to perform a Venn diagram in order to verify whether these most frequent CREs are combined in the same group of genes.

CHAPTER IV

RESULTS AND DISCUSSION

4.1 Differentially Expressed Oligonucleotides in Microarray

The largest part of oligonucleotides of microarrays (95%) were not differentially expressed when compared iron toxicity condition and control condition (Figure 4.1). Considering the up-regulated oligonucleotides, 5,635 represent genes, 7,247 transposable elements (TE), 2,532 correspond to flanking regions of 5’ extremities of TEs, 2,521 correspond to flanking regions of 3' extremities of TEs.

Among the down-regulated oligonucleotides, 204 represent genes, 473 TEs, 91 correspond to flanking regions of 5’ extremities of TEs, 91 correspond to flanking regions of 3' extremities of TEs and 8 are ESTs.

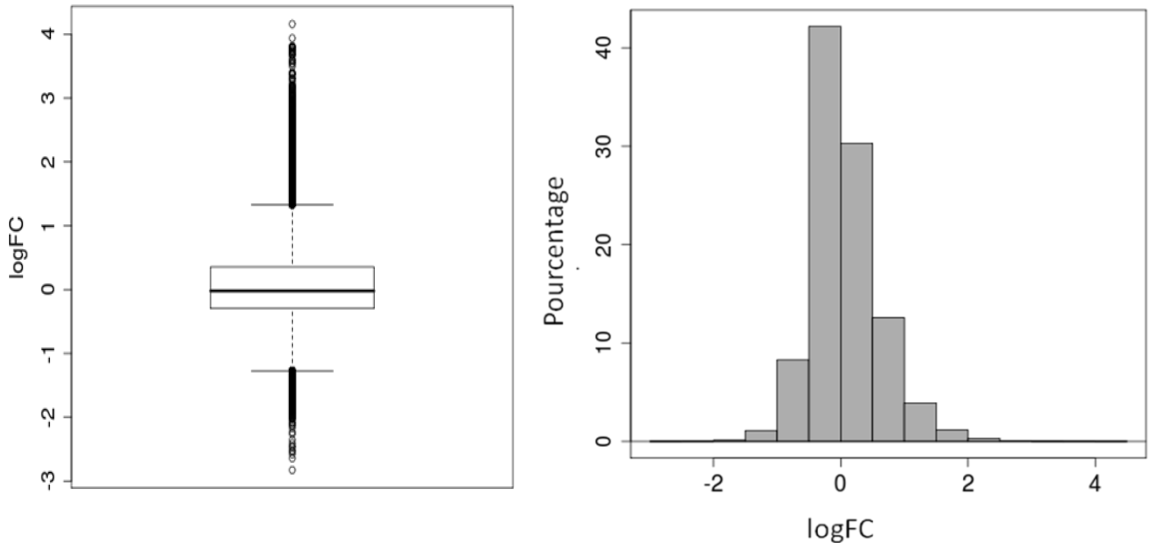

Figure 4.1 Distribuition of Log_2FC of all oligonucleotides of microarray. In the left a boxplot representing all the oligonucleotides of the chip after statistical analysis according to analysis by the Bayesian t-test. Log (FC) = log_2-fold-change.

4.2 Microarray Validation by RT-qPCR

In this study, the correlation coefficient beween microarray and RT-qPCR data were 0.7856 ($P<0.01$), which can be considered a good positive correlation. The Table 4.1 shows relative quantitation obtained by RT-qPCR and the fold change obtained by microarray. It was verified changes in the level of expression, but the same expression pattern was observed for the genes tested in both techniques. Regarding the genes *Os04g0447700* and *Os06g024380*, the expression levels in RT-qPCR were lower than microarray. This could be explained by small changes in the threshold between techniques or small variations in the endogenous gene (GAPDH) between conditions.

Considering that the RT-qPCR quantifies the initial abundance of messenger RNA (mRNA) in the sample, more specifically, sensitively and reproducibly, it is the preferred alternative among the other ways to quantify the final product amplified, since the results of the microarray can be influenced by any errors in each step of this methodology, since the construction of the arrangements to sample preparation (extraction, labeling, hybridization) and obtain images of the microarray (Rajeevan et al., 2001), thus the data generated by microarrays must be validated by independent technical analysis of gene expression, which is currently being used to validate the methodology is the technique of RT-qPCR (Tavares, 2007). However, it is not necessary to check through another appropriate technical analysis of gene expression such as RT-qPCR all differentially expressed genes in microarray, but validate some candidate genes.

4.3 Expression Profile of Genes

There diferentially expressed oligonucleotides correspond to 1,572 up-regulated genes with function described in RAP-DB database

A large number of up-regulated genes encoding transcription factors (TFs) was observed, a total of 165 or 10,5% of a total number of up-regulated genes (Annex 1), most of those represented by the WRKY transcription factor (18 genes) that represents a complex group of TFs involved in many developmental processes and defense responses in plants. In rice, Ricachenevsky et al. (2010) have verified the overexpression of *OsWRKY80* in the leaves of rice (*Oryza sativa* L. ssp. *Indica* cv. BR-IRGA 409) under conditions of iron stress. Another family of TFs that was represented by nine genes is bHLH (helix-loop-helix) and other TF family with expressive number of up-regulated genes was zinc finger. Considering the TFs that are responsive to heavy metal such as cadmium (Cd), DallCorso et al. (2010) reviewed that the main families are WRKY (36 genes) basic leucine Zipper (37 genes) ethylene-responsive factor (ERF) (38 genes) and myeloblastosis protein (MYB) (34 genes) play a significant role in controlling the expression of specific stress-related genes after Cd treatment.

The family of Cytochrome P450 was represented by 49 up-regulated genes (Annex 1 and Figure 4.4) most of them with molecular function monooxygenase activity or iron ion binding. Cytochrome P450 monooxygenases (P450s) play an essential role in the synthesis of lignin, pigments, defense compounds, fatty acids, hormones and signaling molecules in all plant species (Schuler, 1996; Werck-Reichhart et al., 2002; Nielsen and Moller, 2005, Pan et al., 2009). It is estimated that the cytochrome P450 genes correspond to 1% of all genes plant

species (Nelson et al. 2004; Nelson et al. 2008; Mizutani and Ohta, 2010), for example, Arabidopsis, rice, poplar and grape contain 246, 356, 312, and 457 cytochrome P450 genes, respectively.

Additionally, four up-regulated genes coding for metallothionein (MTs) that have a significant role in maintaining intracellular metal homeostasis, metal detoxification and protection against intracellular oxidative damage (Zhou et al., 2006). Sequence analysis of the rice genome revealed that genes encoding putative metallothioneins are fifteen, seven of these genes are on chromosome 12 (RAP-DB build 5). MTs contribute to control the concentration of "free" metals and reactive oxygen species would activate defences, e.g. via the MAPK cascade. These responses would help to regain cellular oxidant and metal homeostasis (Polle and Schützendübel, 2003).

Regarding genes coding for enzymes that are involved in detoxification reactive oxygen species (ROS) that are produced under iron stress toxicity, also known as antioxidant/scavenger enzymes, were also found 11 coding genes to glutathione S-transferases (GSTs) (Annex 1) these enzymes act as scavengers of ROS cell and with the help of glutathione (GSH), reduce peroxides. They were also found other coding genes to antioxidant enzymes such as three genes for superoxide dismutase (SOD), two genes for L-ascorbate peroxidase (APX), four genes similar to peroxidase (PRX) and one gene coding for glutathione reductase (GR). Considering iron toxicity tolerance mechanisms, and having such information it is reasonable to consider that these enzymes are involved in the responses of rice plants that avail themselves of strategy III of iron stress tolerance, which are the plants that allow the uptake of iron in the symplast and are able to accomplish ROS detoxification.

Traditionally, the term oxidative stress is a harmful process with potentially deleterious effects on plant metabolism that have to be avoided by mobilization of the antioxidant defense. However, Kuzniak (2010) point out that recent studies have substantially extended our understanding of the role of ROS in plant biology, suggesting that they are key regulators of biological processes. It is now generally accepted that the effects of ROS result from direct or indirect responses to sensing systems involving antioxidants, rather than from oxidative damage to bio-molecules *per se.*

Under stress, the control of ROS toxicity, simultaneously enables them to act as signaling molecules, requires a complex regulatory network including ROS production, sensor and scavengers systems. The interplay between ROS production and scavenging determines the steady state level of ROS in cells, as well as the ROS signature, i.e. the

duration, localization, and amplitude of ROS signals conditioning stress responses (Mahalingam and Fedoroff 2003; Miller et al. 2008).

Table 4.1 *Locus* identification, level of differential expression of genes in microarray (Log2FC) and relative quantification (RQ expressed in log_2) in RT-qPCR (reverse transcriptase quantitative PCR) in leaves of 18-day-old rice seedlings (*Oryza sativa* ssp. *japonica* cv. Nipponbare) after four days of iron excess exposure, primers sequences and description of gene function.

Locus	**Log_2FC**	**RQ (log_2)**	***Forward Primer***	***Reverse Primer***	***Description***
Os02g0121700	2,14	2,3	AGAGTTTGTTGATCACATCCCTCC	AATCCTTCTTGTGCCTCATCCTT	Terpenoid synthase domain containing protein
Os02g0594800	2,48	3,0	TGAATGCGGTGTATGGACTACCT	CAATGCTCTCCTGTGATCCAAAC	No apical meristem (NAM) protein
Os02g0740700	1,68	2,5	GTGCCGGACTCCATCATGTAC	ACGCCCTTGAAGTTTGGGT	Peptidase M10A and M12B
Os05g0162000	2,25	1,5	TACGGGATGTTTTGAGTTTTCCA	GGCGTCAGGATGTCCATGA	Similar to Peroxidase
Os05g0527000	2,11	3,1	CCGTCATCCGCTTGAATTGA	CGCGTACTTCTTCTTCCCATCC	UDP-glucuronosyl/UDP-glucosyltransferase
Os06g0243801	2,29	-0,8	GTCATTTCTAGGAAGATCATTCAGGAA	GTACATGGCTCTCCTACCTCCAACTA	Hypothetical conserved gene.
Os06g0257450	2,26	3,7	TTTTAGGAGAGCGCGGGAC	TGCGATTCACATGTAGATTCTGTG	Similar to Ribonucleoside-diphosphate reductase
Os08g0467400	1,87	0,8	GCTGGTGGCTTTATTTATATTGCTG	CATTGTCAGGGAAACCAACTGA	Zinc/iron permease family protein.
Os08g0508000	2,58	2,0	GCGGAGAAACGCTACGACA	GTAGGACATGAGGCCGAGGA	Cytochrome P450 family proten
Os04g0447700	1,5	-0,2	ATTGTCAAACGACGACTAATAAGCG	AAGTTTCCCCGAAGTTCATCCT	Similar to Polyketide reductase.
Os12g0601800	1,67	1,2	GTGTATCAGACGCAGCTTCTGC	TGCTGCACTTGGCACAGG	Similar to BZIP transcription factor family
Os06g0141200	-2,54	-2,0	CCAAAGATCGTGAGACGTGA	TCTACCACCCTTGCAACCAT	Similar to RNA-binding protein EWS.
Os05g0506000	-1.02	-1,8	AGGGACCAAATTGCTTGTTG	TGGATGCTTTGCATGATCTC	Similar to MS5-like protein
Os10g0521900	-1,21	-1,6	ATTGGTGCCACTACCTGAGC	ACTAAACCCCTGGGAGGGTA	Peptidase S54, rhomboid protein
Os06g0649000	1,41	2,5	TTAACTGTGTATATTTAGTGATTGATTTTAATTAGC	TCTGGGAGACTCTGAATAGATCTCC	Similar to WRKY transcription factor 28.
Os12g0567800	2,01	1,2	AATCCAGCATTGTGTGTGCG	CATTTACATACAAGCGGTACAACACATA	Plant metallothionein, family 15 protein.
Os12g0567800	2,01	0,5	CAACTGCTAAAGGCCAAGGC	CCACTTGGTTTTCCAGCCATA	Plant metallothionein, family 15 protein.
Os03g0288000	1,12	2,0	GGAGCTACGTGTGCGTATCA	TGCAACTGCTAAGAAGCCATT	Similar to Metallothionein
Os12g0571100	1,42	0,9	CTAAGGCCAAGGCGATCTATGA	TGATTCACACATGGTTGACACAA	Similar to Metallothionein-like protein type 1.
Os05g0399300	3,29	3,0	GlTGAATTGAACGAGCTCCATCA	TTCGCAATTGTCTCAGTATCCG	Similar to Chitinase.
Os12g0571000	2,43	2,5	TACCATGATCCTCGGTGTTG	GGTGCATGCTACGGTCACTA	Metallothionein-like protein type 1.
Os04g0486600	-	-	AAGCCAGCATCCTATGATCAGATT	AAGCCAGCATCCTATGATCAGATT	imilar to Glyceraldehyde-3-phosphate dehydrogenase, cytosolic 3

The processing of ROS involves modifications of redox components, and the adjustment in cellular redox state has been shown as a mechanism by which plants respond to the constantly fluctuating environment (Foyer and Noctor 2005).

In plant cells, the reductive detoxification of ROS is strongly dependent on ascorbate and glutathione being the two main hydrophilic antioxidants and redox buffers (Noctor and Foyer 1998). Glutathione (g-glutamylcysteinyl glycine) is a major non-enzymatic scavenger of ROS due to its unique structural properties, broader redox potential, abundance and wide distribution in plants. However, ascorbate and glutathione are multifunctional compounds with functions extending far beyond the antioxidative system (De Tulio and Arrigoni 2004; Meyer 2008; Noctor 2006).

Two up-regulated genes coding for alternative oxidase 1a and 1b that are involved in a mitochondrial respiration where there exists an alternative respiratory pathway (AOX pathway or cyanide-resistant respiration), which is connected with respiratory chain by an additional terminal oxidase-alternative (AOX) (Vanlerberghe and McIntosh, 1997). The AOX branches from the main respiratory chain at the level of ubiquinone catalyze the four-electron reduction from oxygen to water (Millenaar and Lambers, 2003). Maxwell et al. (1999) verified that the overexpression of AOX, the terminal oxidase in the alternative pathway, reduced significantly ROS production. This suggests that the alternative pathway plays a role in protecting against oxidative stress in plants. In some plant species, it has been proposed that the alternative pathway allows the TCA cycle to continue to operate under conditions where cytochrome pathway has become limiting, thus allowing replenishment of TCA cycle intermediates in action. AOX which aids in reducing ROS production in mitochondria (Robson and Vanlerberghe, 2002).

Regarding the genes of protein modification/post translational modification by ubiquitination, it was observed 1 gene coding for Armadillo-like helical, one similar to cyclophilin-like protein PPIL3b, one tetratricopeptide-like helical domain containing protein, three zinc finger, RING/FYVE/PHD-type and thirteen ubiquitin-conjugating enzyme were found (Annex 1).

They were identified six protein kinases associated with cell wall (WAK), which were identified as transmembrane proteins - receptor-like kinase (RLK) that receive the stimulus by their extracellular domains and transfer signals to its cytoplasmic domain. In *Arabidopsis*

thaliana, Sivaguru et al. (2003) verified that overexpression of WAK1 increased tolerance to aluminum stress.

Another *RLK* gene, *OsSIK1*, which has regions of extracellular leucine-rich repeats has been cloned and characterized in rice by Ouyang et al. (2010) who found tolerance to salinity and drought stress when overexpression of OsSIK1 was induced while, on the other hand, when this gene it was silenced, the sensibility was observed.

We also identified two genes encoding proteins *CDPK*s, which are sensitive kinases that bind to Ca^{2+} and regulate downstream components of signaling pathways for calcium. A study conducted by Asano et al. (2010) in rice under salt stress, demonstrated that overexpression of the gene *OsCPK2*1 – a *CDPK* is involved in positive regulation of signaling pathways to respond to this condition. Another study performed by Asano et al. (2012) demonstrated that rice plants overexpressing *OsCPK12* exhibited increased tolerance to salt stress and sensitivity to abscisic acid (ABA) but increased susceptibility to blast fungus, probably resulting from the repression of ROS production and/or the involvement of OsCPK12 in the ABA signaling pathway because the accumulation of hydrogen peroxide (H_2O_2) in the leaves was less in *OsCPK12* overexpressed plants than in wild-type plants and genes encoding ROS scavenging enzymes (*OsAPx2* and *OsAPx8*) were more highly expressed in this condition. Another three MAP kinases genes (Annex 1) that participate in signaling intracellular cascades were observed.

Regarding sugar signaling, genes of sugar production and sugar regulated genes up-regulated under iron excess in this work, two genes with a function similar to lipoxygenase and another similar to hexose transporter were identified. In *Saccaromices cerevisiae,* in the presence of glucose, the expression of hexose transporters with appropriate affinity and capacity is upregulated through the action of a second glucose signaling pathway. In addition, hexokinase (Hxk2), in response to glucose, translocates to the nucleus, where it interacts with Mig1 (a TF zinc-finger DNA-binding) to form a stable complex that recruits co-repressor proteins (Moreno et al., 2005). *S. cerevisiae* has membrane proteins that act as glucose receptors, glucose binds to these receptors and generates an intracellular signal. In the Rgt2/Snf3 pathway, these two proteins act as glucose receptors. The Rgt2 and Snf3 proteins resemble hexose transporters in structure but have long cytoplasmic tails that are required for signal transduction (Ozcan and Johnston, 1999), glucose binding to these transmembrane proteins initiates signals that activate a pathway that allows hexose transporter gene

expression by repressing Rgt1 function (Ozcan et al., 1996). The Snf3/Rgt2-Rgt1 pathway is responsible for glucose induction of hexose transporter gene expression (Kim and Johnston, 2006).

Another five up-regulated genes belong to a family of citrate transporters (Multi antimicrobial extrusion protein MATE family protein), genes that were found up-regulated in rice roots under stress by cadmium (10mM) and most likely are responsible for the detoxification of iron from the cytoplasm of the cell (Ogawa et al. 2009). In rice the expression level of the *OsFRDL*4 gene in roots was very low in the absence of Al, but was greatly enhanced by Al after short exposure. Furthermore, the *OsFRDL4* expression was regulated by ART1, a C2H2-type zinc finger transcription factor for Al tolerance. In addition, Soares-Bresolin (2010) verified that in iron tolerant genotype (Epagri 108), the expression level of *OsFDRL1* gene was more elevated than in Nipponbare and IRGA-410.

In this study it was identified 11 HSPs (heat shock protein) genes also known as chaperones and among these, five were HSPs70, these proteins have a large importance in response to stress because during stress conditions usually occurs dysfunction in protein conformation. HSP facilitate protein refolding and stabilize polypeptides and membranes. Hsp70 has essential functions in preventing aggregation and assisting refolding of nonnative proteins under stress conditions. Small Hsps, however, are not able to refold nonnative proteins alone, but constitute complexes with unfolded proteins and other Hsps (Wang et al., 2004). Thus, the different classes of chaperones cooperate in cellular protection and play complementary and sometimes overlapping roles in the protection of proteins from stress (Wang et al., 2004; Scarpeci et al., 2008).

They were verified seven up-regulated genes related to ABC transporter. In Arabidopsis, the overexpression of *AtATM3* (*Arabidopsis thaliana* ABC transporter) resulted in an increased tolerance to both Cd and Pb, whereas the gene knockout rendered the plants more sensitive to the heavy metals (Kim et al., 2006). Metals bound to glutathione or phytochelatins are transported into the vacuole via ABC transporters (Rea 1999). Analysis of mutants and transgenic plants provided compelling evidence that the ability to synthesise glutathione is crucial for protection from heavy metals and failure to do so leads to increased sensitivity (Howden et al. 1995, Zhu et al. 1999a,b, Polle and Schützendübel, 2003).

As observed in most adaptative responses, control of gene expression is tightly regulated and has fast response kinetics and controlled reversibility, which enables the cell to

change its transcriptional capacity within minutes in the presence of stress and to return to its basal state after the stress is removed (Nadal et al., 2011)

In *Arabidopsis* Cailliatte et al. (2006) propose that *AtNRAMP6* functions as an intracellular metal transporter, whose presence, when modified, is likely to affect distribution/availability of cadmium within the cell, they verified that *Arabidopsis* transgenic plants overexpressing *AtNRAMP6* were hypersensitive to cadmium, although plant cadmium content remained unchanged. Consistently, a null allele of *AtNRAMP6*, named *nramp6-1*, was more tolerant to cadmium toxicity, a phenotype that was reverted by expressing *AtNRAMP6* in the mutant background.

The genes that have a product that act in the nucleus are involved in a regulation of transcription and/or chromatin remodeling complex such as *Os02g0214900* and *Os02g0215200* that are similar to histone deacetylase HDAC2, these genes belonging a class of enzymes that remove acetyl groups from N6-acetyl-lysine residues on a histone (Ouassi and Ouassi, 2006).

Acetylation levels are the result of the balance of the activities of histone acetyl-transferase (HAT) and HDAC. The levels of histone acetylation play a crucial role in chromatin remodeling and in the regulation of gene transcription (Ropero and Esteller, 2007). The presence of acetylated lysine in histone tails is associated with a more relaxed chromatin state and gene transcription activation, while the deacetylation of lysine residues is associated with a more condensed chromatin state and transcriptional gene silencing (Johnstone, 2002; Iizuka and Smith, 2003). Histone deacetylation increases ionic interactions between the positively charged histones and negatively charged DNA, which yields a more compact chromatin structure and represses gene transcription by limiting the accessibility of the transcription machinery. In addition, histone acetylation has been associated with other genome functions such as chromatin assembly, DNA repair, and recombination (Polo and Almouzni, 2005; Vidanes et al., 2005; Ropero and Esteller, 2007).

4.4 *Gene Ontology*

Regarding to cellular component (Figure 4.2), a large quantity of gene products are located in plastids and mitochondrion followed by nucleus and microbody that according Cammack et al. (2006) are a cytoplasmic organelles, spherical or oval in shape, that are bounded by a single membrane and contain oxidative enzymes, especially those utilizing hydrogen peroxide (H_2O_2) such as peroxissome that detoxificate ROS.

In biological processes (Figure 4.2) the most representative are metabolic process and cellular process, followed by respose to stimulus, localization - that refer to process in which a cell, a substance, or a cellular entity, such as a protein complex or organelle, is transported to, and/or maintained in a specific location (Cammack et al., 2006) and multi-organism process that are physiological interaction between organisms, Any process in which an organism has an effect on another organism of the same or different species.

For molecular function catalytic activity, binding, transcription and transporter regulator activity it was the more representative function.

4.5 Metabolics Pathways of Differentially Expressed Genes are Involved

The majority of up-regulated genes are in the pathaways of biosynthesis of secondary metabolites (113 up-regulated) and biosynthesis of plant hormones (60 up-regulated genes) and among the down-regulated genes the most representative was in methane metabolism (three genes) (Table 4.2).

Another pathway with a expressive number of up-regulated genes is a starch and sucrose metabolism (Figure 4.3) with 29 up-regulated and one down-regulated gene that correspond to is alpha-amylase (Os08g0473600). The fact of this pathway present so many up-regulated genes can be explained by a possible increase of ABA content in rice plants under iron toxicity, for exemple the inhibition of rice growth and the accumulation of storage products that result from heavy metal treatment could be an adaptation mechanism by which plants could maintain a greater viability in this adverse condition and eventually recover if the toxin is removed (Moya et al., 1995).

In this way, Thompson and Couture (1990) found that, in populations of *Selenastrum capricornutum* exposed to Cd, the synthesis of storage products was increased, leading to energy levels (cellular ATP) sufficient to allow the survival of the population while being too low to sustain growth. Because hormones are implicated in the regulation of assimilate metabolism and growth it may be possible that they play a role in the response of plants to heavy metal stress (Thomas, 1986; Dijkstra et al., 1990).

In fact, there is strong evidence that ABA is involved in the adaptation of plants to stresses such as cold or salt (Zeevaart and Creelman, 1988; Walton 1980). Additionally, in deepwater rice, the capacity of plants to elongate rapidly in order to avoid drowning

when they become submerged is thought to be related to the GA to ABA ratio (Hoffmann-Benning and Kende, 1992), which could govern the growth responses in this plant.

In rice, Moya et al. (1995) authors verified that that the applications of GA_3 and abscisic acid (ABA) have a influence on the growth, carbohydrate content, and net photosynthesis of heavy metal-stressed rice plants (*Oryza sativa* cv. Bahía) they verified that treatment of cadmium (0.1 mM) and nickel (0.5 mM) inhibited rice growth and stimulated carbohydrate accumulation, especially in seeds from which seedlings were developing, stems, and first leaves and when ABA (19 µM) was supplied to rice culltures potentiated the effect of heavy metals, inhibiting the growth of young leaves and the translocation of storage products from source to sink organs. Whereas addition of GA_3 to the rice culture solution together with Cd or Ni partially reversed the effects of heavy metals, stimulating growth as well as mobilization of carbohydrate reserves in seeds from which seedlings had developed.

Glutathione metabolism (Table 4.2 and Figure 4.5) with 20 up-regulated genes, is a pathway that is involved in antioxidative system of plants, reduced glutathione (GSH), that is a peptide containing three amino acids (Glu-Cys-Gly), plays a central role by scavenging ROS (Ranieri et al., 2005; Aina et al., 2007). It is generally considered that GSH content positively correlates with metal stress (Tausz et al., 2004). In addition, 11 glutathione S-transferase (GST, EC 2.5.1.18) coding genes were observed. This is a group of dimeric, multifunctional enzymes, that catalyze conjugation of glutathione (GSH) with xenobiotic compounds for detoxification. It has been found that GST involves in GSH-Cd formation, decreasing Cd uptake in yeast cells (Adamis et al., 2004). GST also functions as glutathione peroxidase (GPOX) and participates in plant defense against oxidative stress and toxicity generated from heavy metals (Marrs et al., 1996).

Regarding the phosphatidylinositol (PI) signaling system (Table 4.2 and Figure 4.6) that is a important pathway that is considered critical in plant responses to many environmental factors, seven up-regulated genes were observed: a protein kinase (2.7.11.13), inositol-polyphosphate 5-phosphatase (ec:3.1.3.56), phosphoinositide 5-phosphatase (ec:3.1.3.36), inositol-phosphate phosphatase (ec:3.1.3.25), phosphoinositide phospholipase C (ec:3.1.4.11) phosphatidylinositol 3-kinase (ec:2.7.1.137) and phosphatidate cytidylyltransferasein (ec:2.7.7.41). It has been shown that deficiency of these proteins results

in exceptional physiological phenomena such as changed cell response to hormone treatments, and someabiotic stresses, which perhaps even involves the interaction with other signaling pathways such as the calcium-related signaling network (Berridge et al., 1998; Carafoli, 2002; Lin et al., 2004).

In *Arabidopsis thaliana*, Lin et al. (2004) tested normal leaf, stem and flower tissues, and leaves from plants treated with various hormones (auxin, cytokinin, gibberellin, abscisic acid and brassinosteroid) or environmental factors (temperature, calcium, sodium, drought, salicylic acid and jasmonic acid) and verified that many PI pathway-related genes were differentially expressed under these experimental conditions and that the in particular, the different isoforms of each family were specifically expressed in many cases, suggesting their involvement in tissue specificity and cellular responses to environmental conditions.

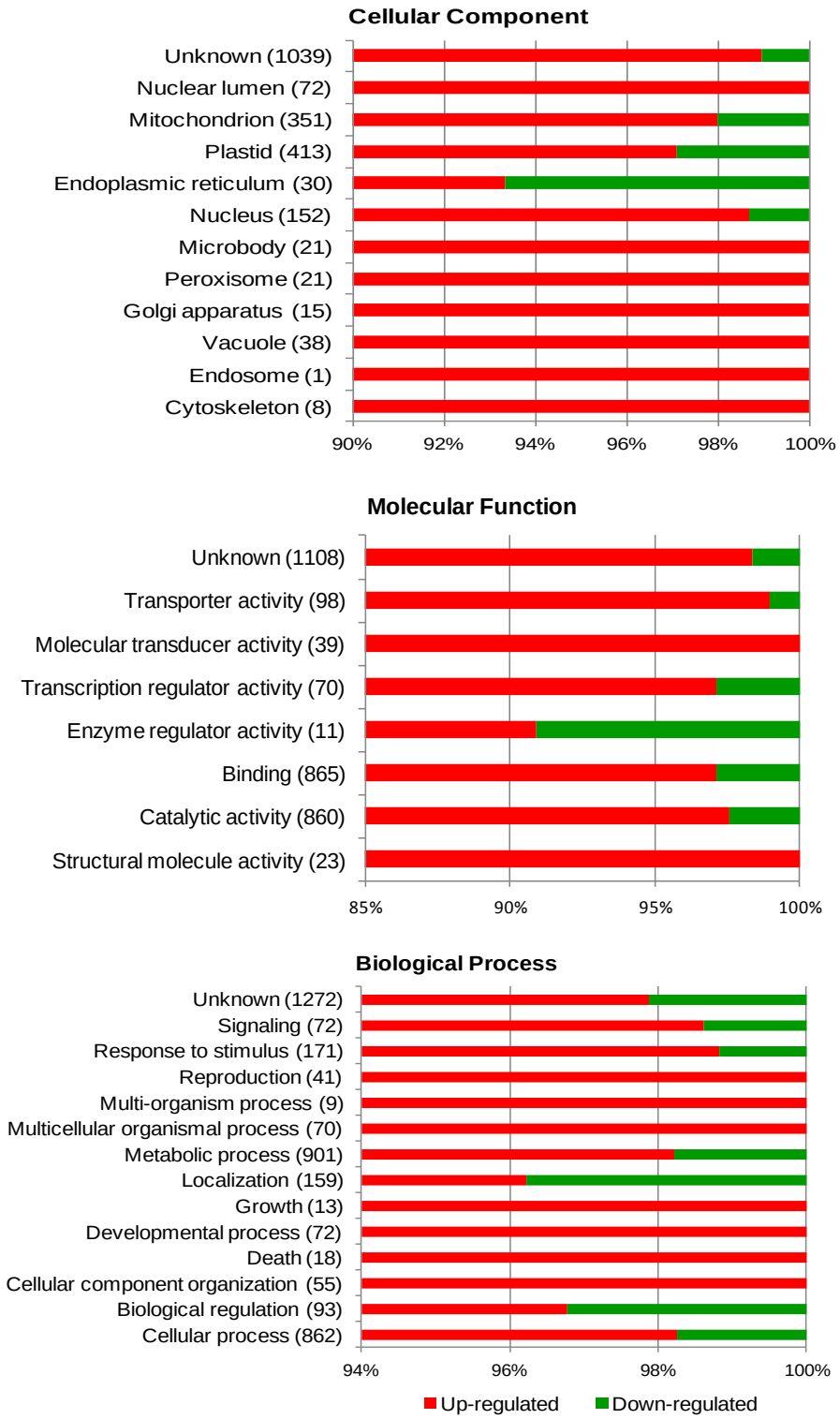

Figure 4.2 Cumulative percentage of up-regulated and down-regulated genes in leaves of 18-day-old rice seedlings (*Oryza sativa* ssp. *japonica* cv. Nipponbare) after four days of iron excess exposure . Gene ontology generated by GO Slim. Biological Process and Molecular Function level 2 and Cellular Component level 5. The total number of differentially expressed genes for each functional category is shown in parenthesis.

Table 4.2 Number of up and down-regulated genes in leaves of 18-day-old rice seedlings (Oryza sativa ssp. japonica cv. Nipponbare) after four days of iron excess exposure, and its respective metabolic pathway generated by Kegg (Kyoto Encyclopedia of Genes and Genomes).

Pathway	Up-regulated	Down-regulated
Alanine, aspartate and glutamate metabolism	11	
alpha-Linolenic acid metabolism	11	
Amino sugar and nucleotide sugar metabolism	16	
Aminoacyl-tRNA biosynthesis	6	
Aminobenzoate degradation	4	1
Arachidonic acid metabolism	4	
Arginine and proline metabolism	12	1
Ascorbate and aldarate metabolism	10	1
Benzoate degradation	4	
Benzoxazinoid biosynthesis	2	
beta-Alanine metabolism	11	1
Biotin metabolism	1	
Butanoate metabolism	7	
Butirosin and neomycin biosynthesis	1	
C5-Branched dibasic acid metabolism	1	
Caffeine metabolism	2	
Caprolactam degradation	1	
Carbon fixation in photosynthetic organisms	14	
Carbon fixation pathways in prokaryotes	9	
Carotenoid biosynthesis	2	
Chloroalkane and chloroalkene degradation	2	1
Chlorocyclohexane and chlorobenzene degradation	2	
Citrate cycle (TCA cycle)	10	
Cyanoamino acid metabolism	4	
Cysteine and methionine metabolism	12	
D-Glutamine and D-glutamate metabolism	2	
Diterpenoid biosynthesis	7	
Drug metabolism - cytochrome P450	21	1
Drug metabolism - other enzymes	8	
Ether lipid metabolism	2	
Ethylbenzene degradation	1	
Fatty acid biosynthesis	3	
Fatty acid elongation	2	
Fatty acid metabolism	15	1
Flavone and flavonol biosynthesis	1	
Flavonoid biosynthesis	2	
Fluorobenzoate degradation	2	
Fructose and mannose metabolism	6	

... continuation

Pathway	Up-regulated	Down-regulated
Galactose metabolism	10	
Geraniol degradation	3	
Glucosinolate biosynthesis	2	
Glutathione metabolism	20	
Glycerolipid metabolism	10	1
Glycerophospholipid metabolism	11	
Glycine, serine and threonine metabolism	12	
Glycolysis / Gluconeogenesis	16	1
Glycosaminoglycan degradation	3	
Glycosphingolipid biosynthesis - ganglio series	3	
Glycosphingolipid biosynthesis - globo series	1	
Glyoxylate and dicarboxylate metabolism	15	
Histidine metabolism	1	1
Inositol phosphate metabolism	6	
Isoflavonoid biosynthesis	1	
Isoquinoline alkaloid biosynthesis	6	
Limonene and pinene degradation	2	1
Linoleic acid metabolism	7	
Lipoic acid metabolism	1	
Lysine biosynthesis	4	
Lysine degradation	7	1
Metabolism of xenobiotics by cytochrome P450	15	
Methane metabolism	28	5
Naphthalene degradation	1	
N-Glycan biosynthesis	1	
Nicotinate and nicotinamide metabolism	4	
Nitrogen metabolism	9	1
Novobiocin biosynthesis	2	
One carbon pool by folate	3	
Other glycan degradation	6	
Other types of O-glycan biosynthesis	1	
Oxidative phosphorylation	10	
Pantothenate and CoA biosynthesis	6	
Pentose and glucuronate interconversions	8	1
Pentose phosphate pathway	7	
Phenylalanine metabolism	20	3
Phenylalanine, tyrosine and tryptophan biosynthesis	14	
Phenylpropanoid biosynthesis	16	3
Phosphatidylinositol signaling system	7	
Porphyrin and chlorophyll metabolism	6	1
Primary bile acid biosynthesis	1	

... continuation

Pathway	Up-regulated	Down-regulated
Propanoate metabolism	8	1
Purine metabolism	35	
Pyrimidine metabolism	11	
Pyruvate metabolism	11	1
Retinol metabolism	4	
Riboflavin metabolism	2	1
Selenocompound metabolism	1	
Sphingolipid metabolism	7	
Starch and sucrose metabolism	29	1
Steroid biosynthesis	3	
Steroid hormone biosynthesis	4	
Stilbenoid, diarylheptanoid and gingerol biosynthesis	1	
Streptomycin biosynthesis	2	
Styrene degradation	1	
Sulfur metabolism	6	
Synthesis and degradation of ketone bodies	2	
T cell receptor signaling pathway	5	
Taurine and hypotaurine metabolism	2	
Terpenoid backbone biosynthesis	4	
Thiamine metabolism	10	
Toluene degradation	2	
Tropane, piperidine and pyridine alkaloid biosynthesis	8	
Tryptophan metabolism	9	
Tyrosine metabolism	13	1
Ubiquinone and other terpenoid-quinone biosynthesis	4	
Valine, leucine and isoleucine biosynthesis	4	
Valine, leucine and isoleucine degradation	17	1
Various types of N-glycan biosynthesis	1	
Vitamin B6 metabolism	3	
Zeatin biosynthesis	2	
Biosynthesis of alkaloids derived from histidine and purine	23	
Biosynthesis of alkaloids derived from ornithine, lysine and nicotinic acid	30	
Biosynthesis of alkaloids derived from shikimate pathway	36	
Biosynthesis of alkaloids derived from terpenoid and polyketide	22	
Biosynthesis of phenylpropanoids	48	
Biosynthesis of plant hormones	60	
Biosynthesis of secondary metabolites	113	
Biosynthesis of terpenoids and steroids	27	
Biosynthesis of type II polyketide products	1	
Biosynthesis of unsaturated fatty acids	6	

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Pathway	Up-regulated	Down-regulated
Metabolic pathways	223	
Microbial metabolism in diverse environments	73	
Cumulative total	**1410**	**33**

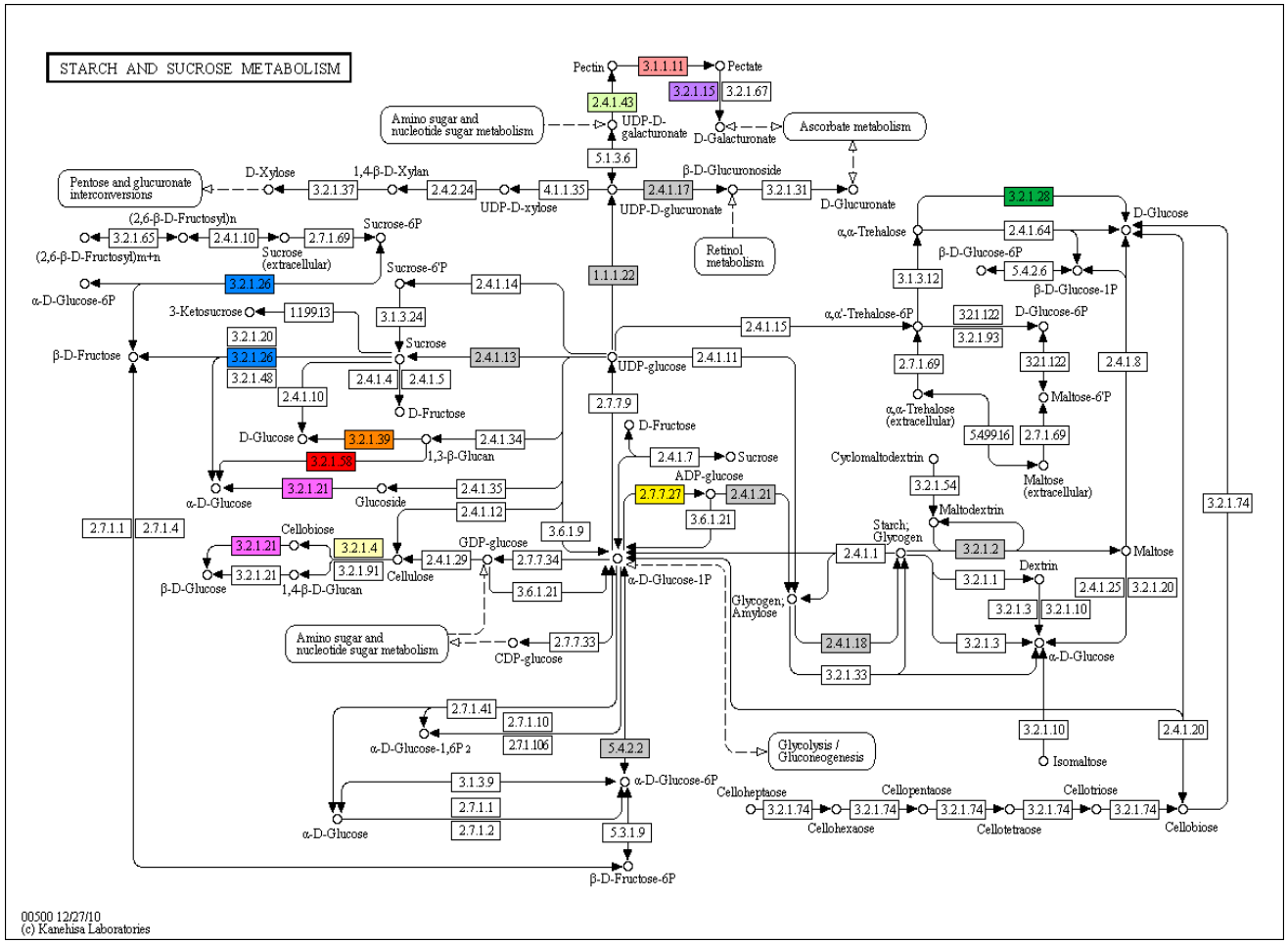

Figure 4.3 Up-regulated genes belonging to starch and sucrose methabolism in 18-day-old rice leaves (*Oryza sativa* ssp. *japonica* cv. Nipponbare) of seedlings after four days of iron excess exposure, and its respective metabolic pathway generated by Kegg (Kyoto Encyclopedia of Genes and Genomes). Colored boxes indicate the differents enzymes corresponding to up-regulated genes. Red ec:3.2.1.58 - glucan 1,3-beta-glucosidase (30), Yellow ec:2.7.7.27 - glucose-1-phosphate denylyltransferase (2); Orange ec:3.2.1.39 - glucan endo-1,3-beta-D-glucosidase (3); Green ec:3.2.1.28 - alpha,alpha-trehalase Blue ec:3.2.1.26 - beta-fructofuranosidase; Pink ec:3.2.1.21 - beta-glucosidase (2); Violet ec:3.2.1.15 - polygalacturonase (3); Light-red ec:3.1.1.11 - pectinesterase; Light-green ec:2.4.1.43 - polygalacturonate 4-alpha-galacturonosyltransferase (2); Light-yellow ec:3.2.1.4 - cellulose (2); Gray ec:3.2.1.2 - beta-amylase; Gray ec:2.4.1.21 - starch synthase (2); Gray ec:2.4.1.18 - 1,4-alpha-glucan branching grayec:2.4.1.17 - glucuronosyltransferase; Gray ec:2.4.1.13 - sucrose synthase; Gray ec:5.4.2.2 - phosphoglucomutase; Gray ec:1.1.1.22 - UDP-glucose 6-dehydrogenase. The numbers in parentheses indicate the number of different genes coding for the same enzyme.Pathway generated by Kegg Database (Kanehisa et al. 2011).

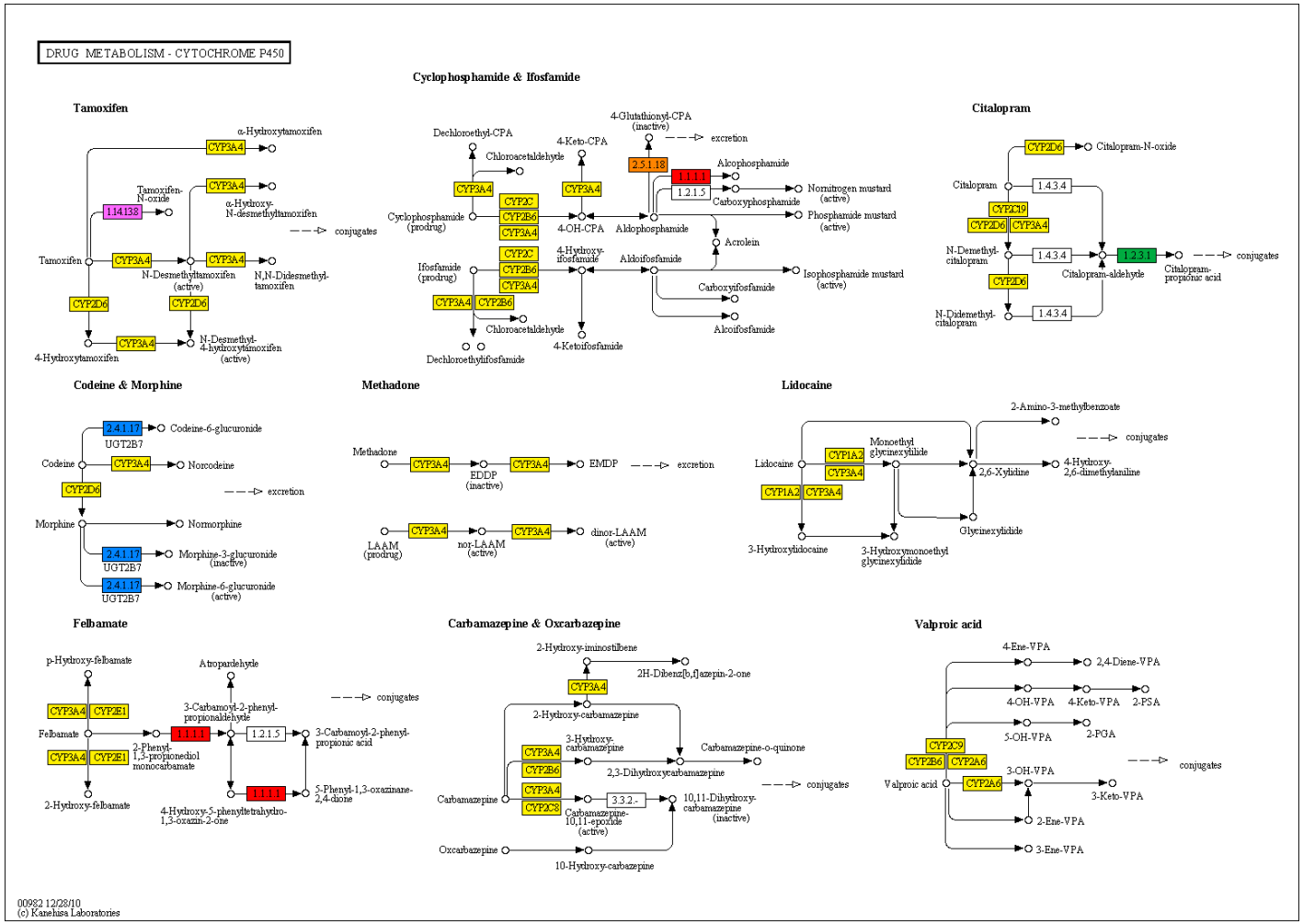

Figure 4.4 Up-regulated genes belonging to drug methabolism – cytochrome P450 in leaves of 18-day-old rice seedlings (*Oryza sativa* ssp. *japonica* cv. Nipponbare) after four days of iron excess exposure . Colored boxes indicate the differents enzymes corresponding to up-regulated genes: Red ec:1.1.1.1 - alcohol dehydrogenase(1); Yellow ec:1.14.14.1 - unspecific monooxygenase (2); Orange ec:2.5.1.18 - glutathione transferase (11); Green ec:1.2.3.1 - aldehyde oxidase (3); Blue ec:2.4.1.17 - glucuronosyltransferase (1); Pink ec:1.14.13.8 - flavin-containing monooxygenase (3). The numbers in parentheses indicate the number of different genes coding for the same enzyme. Pathway generated by Kegg Database (Kanehisa et al. 2011).

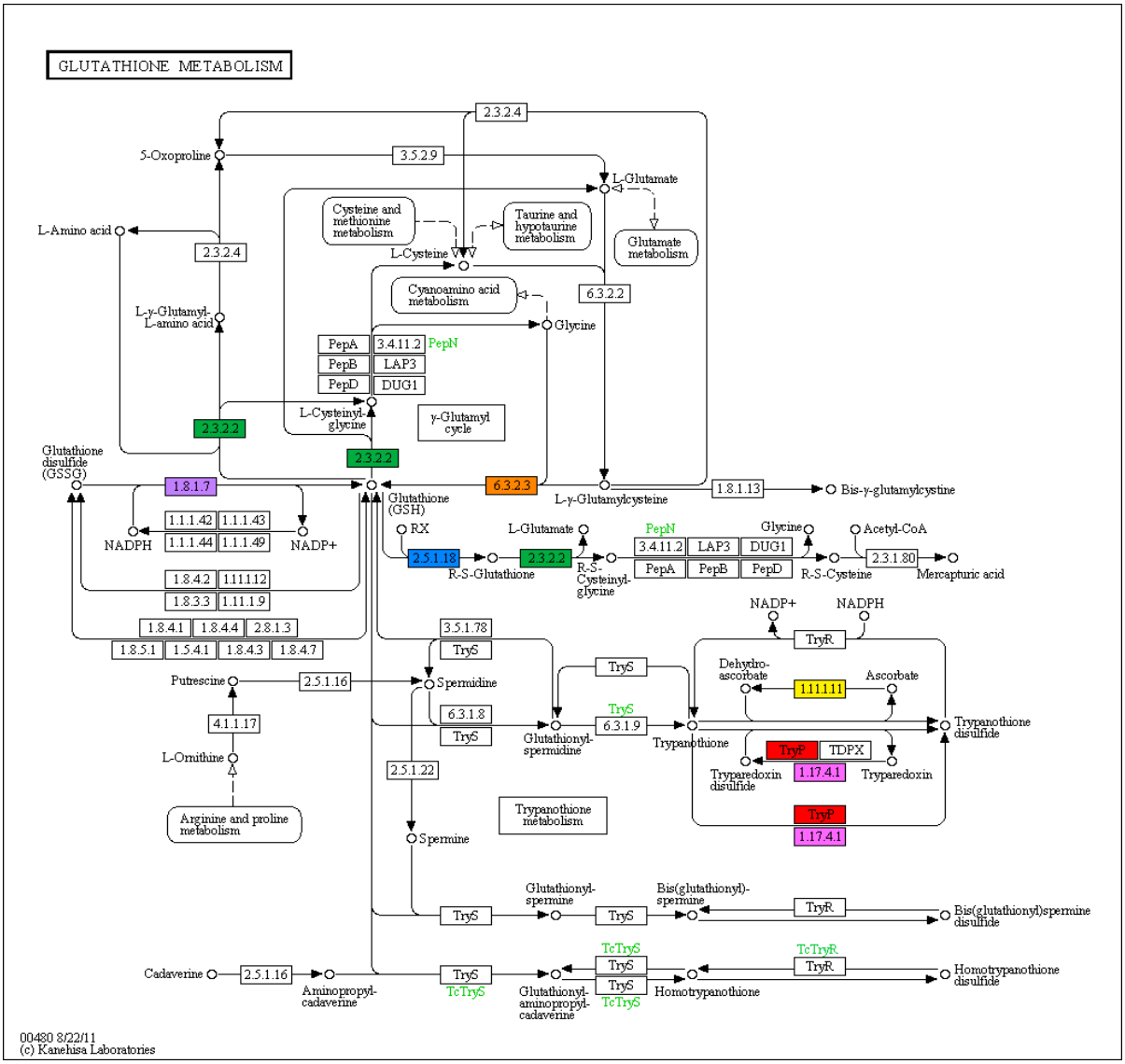

Figure 4.5 Up-regulated genes belonging to glutathione methabolism regulated genes belonging to drug methabolism pathway in 18-day-old rice leaves (*Oryza sativa* ssp. *japonica* cv. Nipponbare) of seedlings after four days of iron excess exposure. Colored boxes indicate the differents enzymes corresponding to up-regulated genes. red ec:1.11.1.15 - peroxiredoxin; Yellow ec:1.11.1.11 - L-ascorbate peroxidase (2); Orange ec:6.3.2.3 - glutathione synthase; Green ec:2.3.2.2 - gamma-glutamyltransferase; Blue ec:2.5.1.18 - glutathione transferase (11); Pink ec:1.17.4.1 - ribonucleoside-diphosphate (3); Violet ec:1.8.1.7 - glutathione-disulfide reductase. The numbers in parentheses indicate the number of different genes coding for the same enzyme. Pathway generated by Kegg Database (Kanehisa et al. 2011).

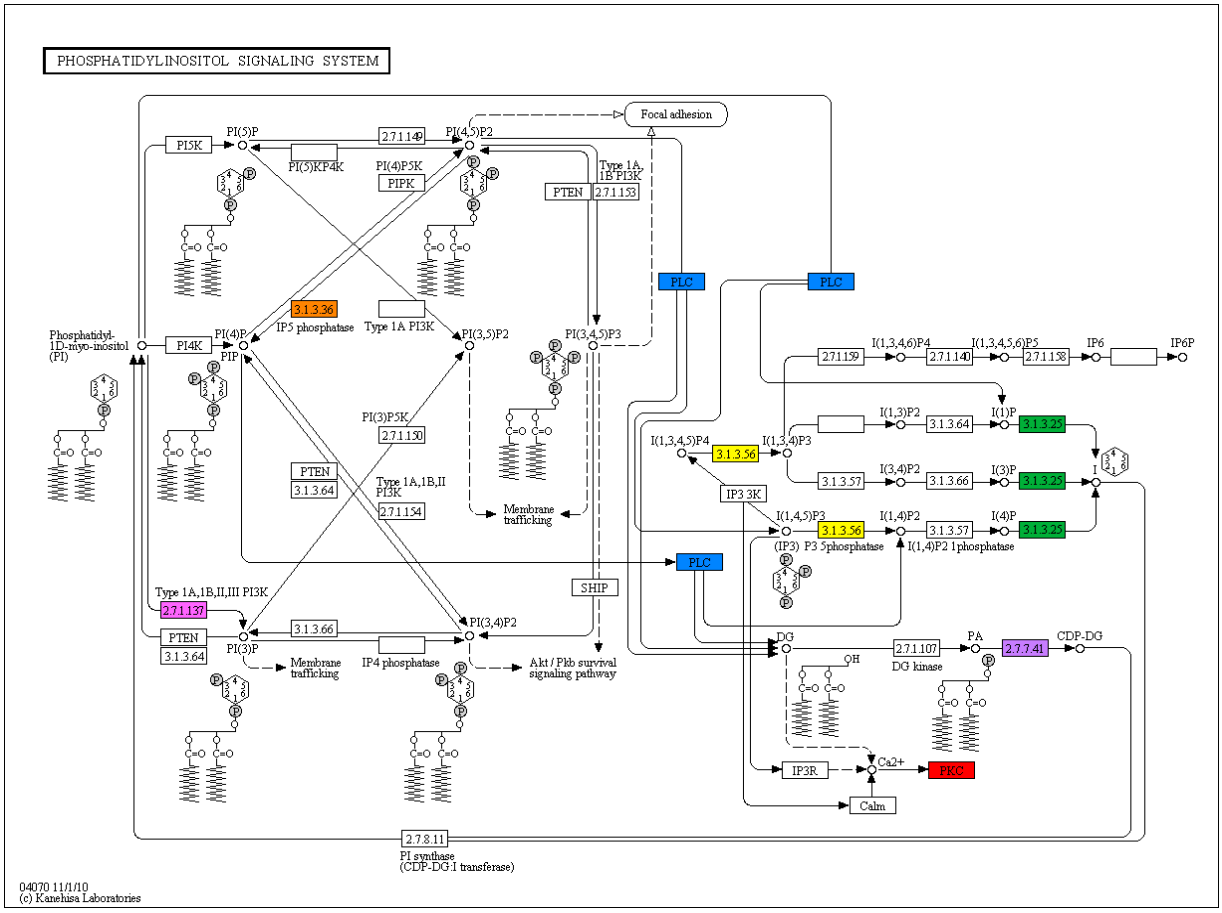

Figure 4.6 Up-regulated genes belonging to phosphatidylinositol signaling system in 18-day-old rice leaves (*Oryza sativa* ssp. *japonica* cv. Nipponbare) of seedlings after four days of iron excess exposure. Colored boxes indicate the differents enzymes corresponding to up-regulated genes: red ec:2.7.11.13 - protein kinase; yellow ec:3.1.3.56 - inositol-polyphosphate 5-phosphatase; orange ec:3.1.3.36 - phosphoinositide 5-phosphatase; green ec:3.1.3.25 - inositol-phosphate phosphatase; blue ec:3.1.4.11 - phosphoinositide phospholipase C; pink ec:2.7.1.137 - phosphatidylinositol 3-kinase; violet ec:2.7.7.41 - phosphatidate cytidylyltransferase. The numbers in parentheses indicate the number of different genes coding for the same enzyme. Pathway generated by Kegg Database (Kanehisa et al. 2011).

4.6 Quantification of Micronutrients in the Tissue of Rice Shoots

They were verified significant differences (p=0.00374) between iron content in leaves of 18-day-old rice seedlings (*Oryza sativa* ssp. *japonica* cv. Nipponbare) after four days of iron excess exposure (Table 4.3). On the other hand, for micronutrients such as manganese, cooper and zinc was not verified significant differences (p>0.05) between control and iron toxicity conditions. These results indicate that 18-day-old rice seedlings of cv. Nipponbare cultivated in iron excess solution (7 mM of $FeSO_4.7H_2O$) absorbed more than 2x the amount of iron than the seedlings in control condition (optimum amount of iron).

Soares-Bresolin (2010) verified that in 31-day-old plants after three days of exposition to concentration of 2000 mg L^{-1} of $FeSO_4.7H_2O$, the tolerant and sensitive genotypes accumulated significantly more content of iron than in a control condition, on the other hand, sensible genotypes accumulated ca. 50% more iron than tolerant, this author also verified an increase in manganese and zinc content under iron toxicity with a positive correlation with increase in iron content.

Table 4.3 Means of micronutrients content in leaves of 18-day-old rice seedlings (*Oryza sativa* ssp. *japonica* cv. Nipponbare) after four days of iron excess exposure. Different letters indicate differences in means between control and iron toxicity conditions by ANOVA F-test.

Condition	Micronutrients content (mg kg^{-1})			
	Manganese	Cooper	Zinc	Iron
Control	500.50 a	27.72 a	91.68 a	795.75 b
Iron toxicity	527.87 a	26.38 a	105.04 a	1927.12 a

4.7 Occurrence of cis-Regulatory Elements (CREs) in Promoters of Up-Regulated Genes

They were verified 330 CREs with significant occurrence ($P \leq 0.05$) in the promoters of 1.569 up-regulated genes. The number of different occurrences of CREs in promoter genes ranged from one to 35 (Figures 4.7 and 4.8). Considering the complex regulation group of genes, they observed 81 genes (those which present from 24 to 35 different CREs in the promoter region) and 99 genes the simple regulation group (whose which present from seven to one different CRE in the promoter region). They were observed 180 and 257 CREs in group of genes with simple and complex regulation respectively, and of these, 11 CREs are

unique from genes with simple regulation, 185 occur in both groups, and 88 are unique from genes with complex regulation.

Considering the biological processes (BPs) in which these genes participate (Figure 4.9) the majority of BPs generated at level 3 have a simple regulation especially when it comes to the cellular organization in general. No pattern of complex or simple regulation was found for genes that are responsive to stresses such as response to stimuli (abiotic, biotic, endogenous), response to stress and oxidation reduction processes.

Regarding molecular functions (MFs) (Figure 4.10) the most part of MFs observed represent genes with both simple and complex regulation. However signal transcription activator activity (Similar to WRKY transcription factor 63), ribonucleoprotein binding, and metal cluster binding have simple regulation only, and lipid binding, cofactor transport activity, isomerase activity, oxygen and pigment binding and peroxidase activity have complex a regulation.

Taking into account the number of promoter genes where each CRE is significantly present, it was found a variation of CREs which occurs from one to 346 different genes (Figure 4.8). Eighteen CREs that are present from 208 to 246 different genes, these CREs are binding sites for MYB transcription factor (MYB2AT and MYBGAHV), BZIP (ACGTABOX, HEXMOTIFTAH3H4) and ARF1 (ARFAIT).

Additionally, among the ABA responsive CREs we identified 21 out of 28 CREs that have at least one significant occurrence in promoters (1 kbp upstream region) of 435 up-regulated genes in response to iron toxicity (this represents ca. 28% of up-regulated genes). The CREs ACGTABREMOTIFA2OSEM (TACGTA) and ABRERATCAL are present in 201 and 183 promoters respectively (Annex 3). The 435 up-regulated genes include kinases, transcription factors, genes involved in ROS detoxification among others.

That it is important to determine *cis*-regulatory elements in the stress-responsive promoters to understand the molecular switches of stress-inducible genes (Yamaguchi-Shinozaki and Shinozaki, 2005). The accurate identification of promoter regions transcription start sites (TSSs) is an important step for *in-silico* gene discovery and understanding of the transcription regulation mechanisms. Every eukaryotic gene has a core promoter region in the 5′ untranslated region (UTR) that contains at a minimum a TSS signal. Most eukaryotic genes are transcribed by RNA Polymerase II which binds at the TSS. Promoter regions are found to share common subtle patterns or models known as motifs that act as binding sites where other

transcription factors attach to facilitate or regulate transcription. For example, up to 80% of human promoters contain an initiator element (Inr) located at the transcription start site with a consensus sequence of YCAYYYYY, where Y represents a pyrimidine base C or T (Suzuki et al., 2001).

Roughly 30% of human core promoters are found to contain a TATA box at position of −20 to −30 from the TSSs with the consensus TATAAA (Suzuki et al., 2001). The TATA box tends to be surrounded by GC rich sequences. Promoter signals with greater variation are found in the promoter region proximal to the TSS, where motifs such as the CAAT, GC, E, and GATA boxes are located (Bajic et al., 2004).

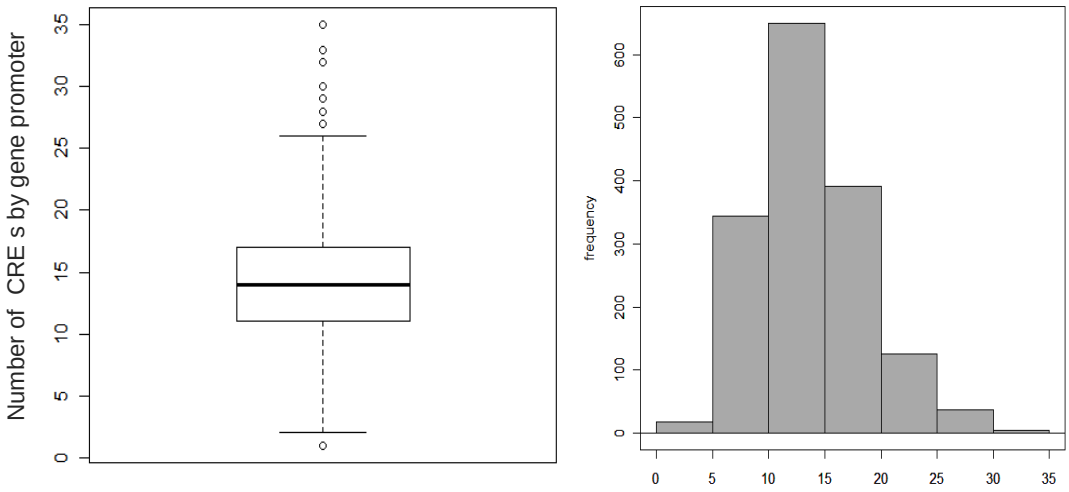

Figure 4.7 a) Boxplot with a number of occurrences of cis-regulatory elements (CREs) by promoters of 1.569 up-regulated genes in leaves of 18-day-old rice seedlings (*Oryza sativa* ssp. *japonica* cv. Nipponbare) after four days of iron excess exposure; b) Histogram represents the frequency of occurrences of CREs by promoters of 1.569 up-regulated genes.

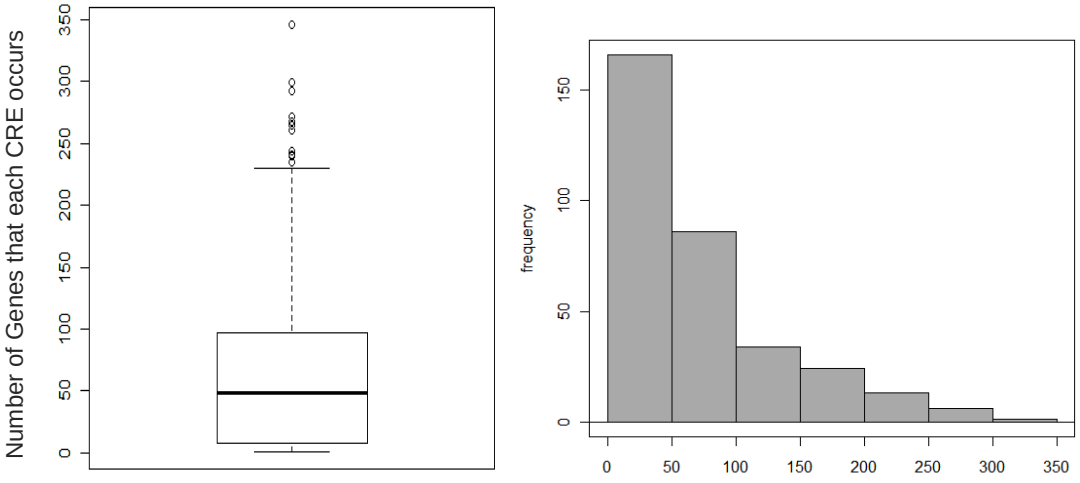

Figure 4.8 a) Boxplot with a number of 1.569 promoter of genes up-regulated in leaves of 18-day-old rice seedlings (*Oryza sativa* ssp. *japonica* cv. Nipponbare) after four days of iron excess exposure where each CRE is significantly present; b) Histogram that represents the distribution of frequency of rice promoter of genes up-regulated under iron excess genes where each CRE is significantly present.

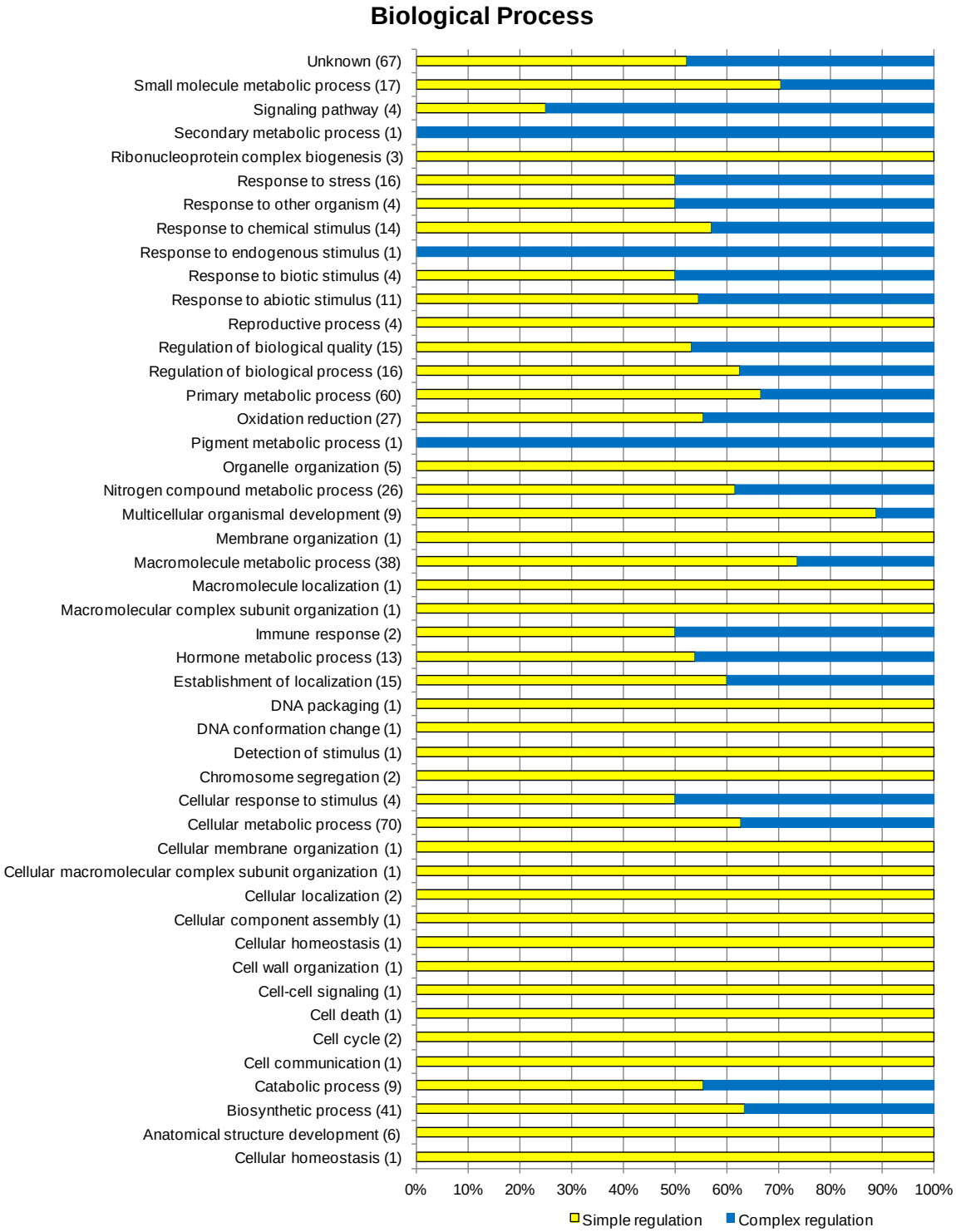

Figure 4.9 Cumulative percentage for gene ontology – biological process at level 3 for up-regulated genes that have a simple or complex regulation in leaves of 18-day-old rice seedlings (*Oryza sativa* ssp. *japonica* cv. Nipponbare) after four days of iron excess exposure. Gene ontology generated by GO Slim. Molecular Function level 3 and Cellular Component level 5. The total number of differentially expressed genes for each functional category is shown in parenthesis.

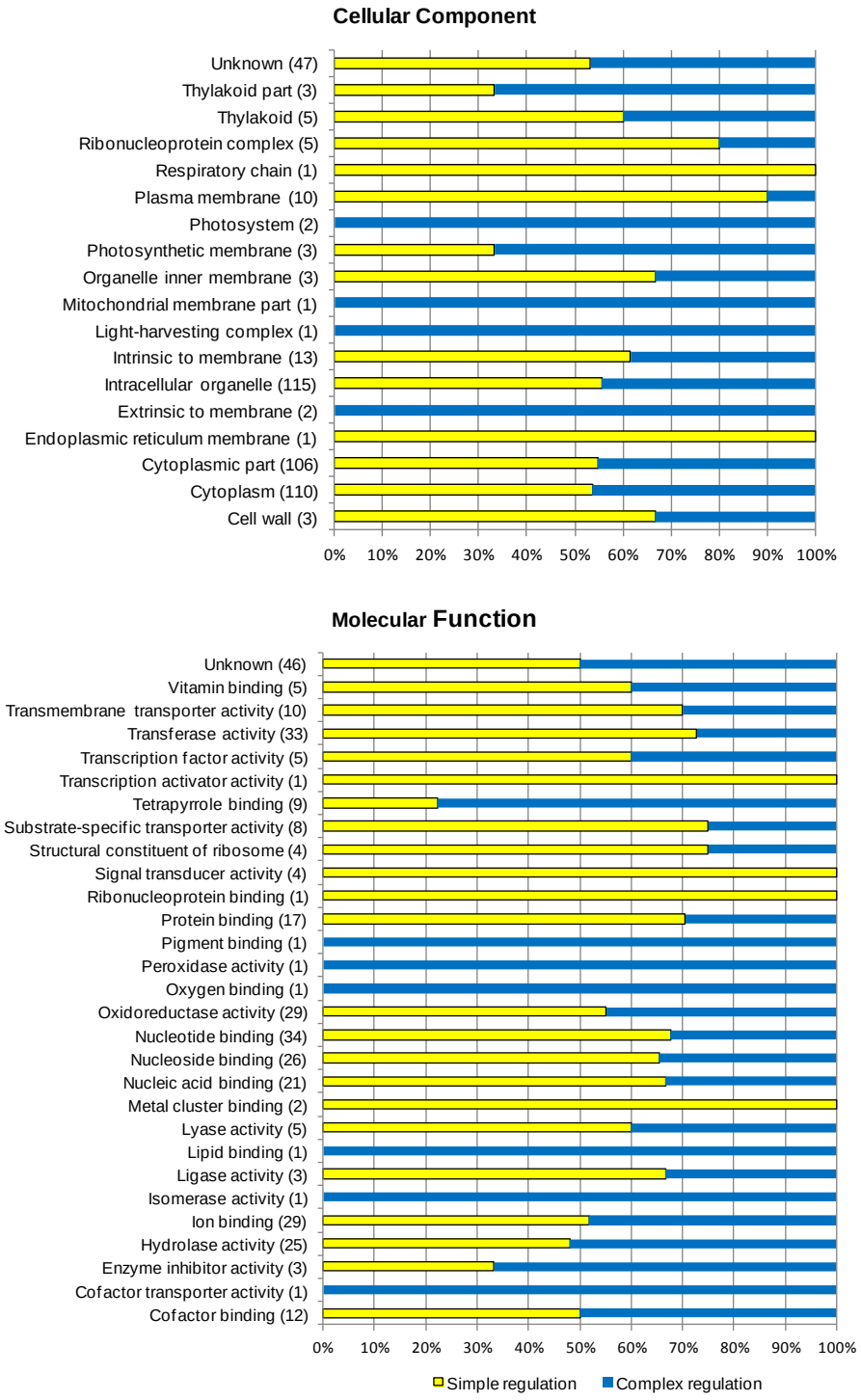

Figure 4.10 Cumulative percentage for gene ontology for up-regulated genes that have a simple or complex regulation in leaves of 18-day-old rice seedlings (*Oryza sativa* ssp. *japonica* cv. Nipponbare) after four days of iron excess exposure. Gene ontology generated by GO Slim. Molecular Function level 3 and Cellular Component level 5. The total number of differentially expressed genes for each functional category is shown in parenthesis.

4.8 Expression Profile of Transposable Elements

A large transcriptional activity of LTR retrotransposons was observed, the majority was up-regulated and the most representative class was *Ty3/Gypsy* (Figure 4.11). Regarding expression of LTR retrotransposons, 302 were down-regulated (53 *Ty1/Copia,* 172 *Ty3/Gypsy* and 77 unclassified), and 4342 up-regulated (466 Ty1*/Copia,* 2276 *Ty3/Gypsy* and 1600 unclassified). The fact that *Ty3/Gypsy* present a higher number of families when compared with *Ty1/Copia* is due to abundance of these elements in the genome, since *Gypsy-like* elements are > 4x more abundant than *Copia-like* elements (Gao et al. , 2004).

Some families of retrotransposons *Ty3/Gypsy* class have a large number of up-regulated sequences than others (Table 4.4) for exemple, Osr26_AP001111-0#LTR/Gypsy and Os5_08_1L#LTR/Gypsy that have 99 and 93 up-regulated copies, respectively. Regarding the retrotransposons *Ty1/Copia* (Table 4.5) the families Os6_08_2L#LTR/Copia and COPIA1-LTR_OS#LTR/Copia with greater number of up-regulated sequences, 35 and 71 sequences respectively.

Presumably, despite the host organism negatively regulates proliferation of LTR retrotransposons, the transcriptional activity of retrotransposons suggests that part of this regulation is likely to take place at a post-transcriptional level (Mourier and Willerslev, 2010).

Several studies emphasize the transcriptional activity of LTR retrotransposons, in rice, Picault et al. (2009) studied transcriptional activity of LTR retrotransposons in calli compared with embryos and verified that *Gypsy-like* presented 8 and 5 down and up-regulated families respectivelly while *Copia-like* presented 4 and 6 down and up-regulated families respectivelly. In embryo, endosperm, ovary, pericarp, female flower, male flower, leaves, root and shoot apical meristem of maize, Vicient (2010) showed that transcriptional activity of the *gypsy-like* retrotransposons is higher in all tissues when compared to other classes.

In fission yeast *Schizosaccharomyces pombe* Mourier and Willerslev (2010) showed a large transcriptional activity in LTR retrotransposons during growth phase in rich medium and although the redundancy of retrotransposon sequences makes it difficult to assess which elements are transcriptionally active, but data strongly indicates that only a subset of the LTR retrotransposons contribute significantly to the detected transcription. A considerable level of reverse strand transcription is also detected. In addition, transcriptome data collected during

meiosis suggests that transcription of solitary LTRs is correlated with the transcription of nearby protein-coding genes.

Transcriptionally and transpositionally active retrotransposons have been shown to be capable of inducing random disruption of genes in various plants, which is most typically evidenced by *Tos17* of rice (Hirochika 2001; Miyao et al. 2007).

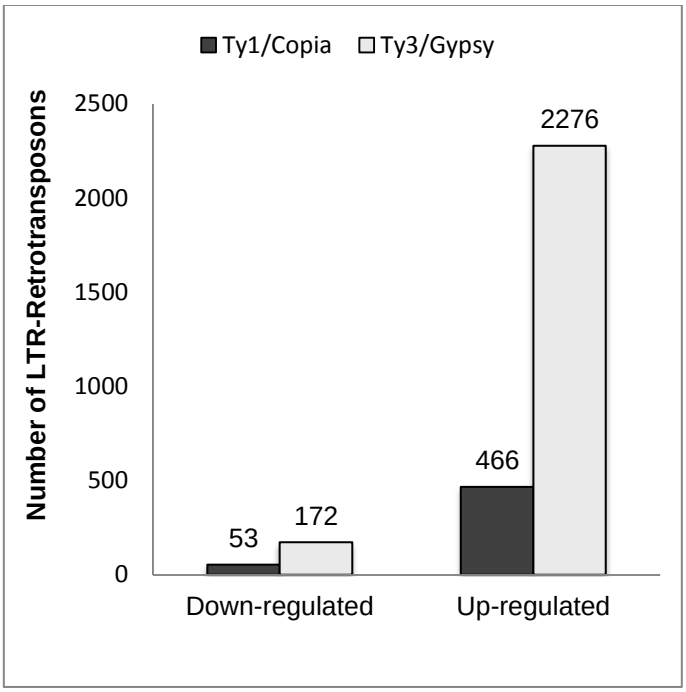

Figure 4.11 Groups of LTR retrotransposon (*Ty3/Gypsy* and *Ty1/Copia* differentially expressed in leaves of 18-day-old rice seedlings (*Oryza sativa* ssp. *japonica* cv. Nipponbare) after four days of iron excess exposure. Unclassified: down-regulated 77 TEs, and up-regulated 1600 TEs.

Table 4.4 Number of copies of LTR retrotransposons *Ty3/Gypsy* class up-regulated (up) and down-regulated (down) in leaves of 18-day-old rice seedlings (*Oryza sativa* ssp. *japonica* cv. Nipponbare) after four days of iron excess exposure.The copies are located in differents positions of the same or different chromosomes.

LTR-retrotranposon	Up	Down	LTR-retrotranposon	Up	Down
ATLANTYS-I_OS#LTR/Gypsy	10	3	Os3S_22L#LTR/Gypsy	4	
ATLANTYS-LTR_OS#LTR/Gypsy	34	1	Os3S_23L#LTR/Gypsy	10	
BAJIE_LTR#LTR/Gypsy	22		Os3S_3L#LTR/Gypsy	3	
CRM-I_OS#LTR/Gypsy	2	1	Os3S_9L#LTR/Gypsy	32	6
GypsO_I#LTR/Gypsy	3	2	Os4_01_1L#LTR/Gypsy	16	
GypsO_LTR#LTR/Gypsy	16	1	Os4_03_2L#LTR/Gypsy	28	14
GYPSY1-I_OS#LTR/Gypsy	1	1	Os4_03_4L#LTR/Gypsy	3	
GYPSY1-LTR_OS#LTR/Gypsy	2		Os4_05_3L#LTR/Gypsy	21	
huck_573L14-2#LTR/Gypsy	1		Os4_06_3L#LTR/Gypsy	42	16
ifisi_84L17-1#LTR/Gypsy	4		Os4_07_1L_WD#LTR/Gypsy	40	4
ifisi_ac079037-1#LTR/Gypsy	8		Os4_09_1L#LTR/Gypsy	1	
ifisi_AP003348-1#LTR/Gypsy	2		Os4_11_1L#LTR/Gypsy	20	
ifisi_AP005618-1#LTR/Gypsy	3		Os4_11_2L#LTR/Gypsy	2	
ORSgTERT00200043_11326#LTR/Gypsy	1		Os4_12_1L_WD#LTR/Gypsy	3	
ORSgTERT00200045_11280#LTR/Gypsy	2		Os4_18_2L#LTR/Gypsy	22	7
ORSgTERT00200072_11305#LTR/Gypsy	2	1	Os5_01_1L#LTR/Gypsy	1	
ORSgTERT00200108_11304#LTR/Gypsy	1		Os5_02_1L#LTR/Gypsy	5	
ORSgTERT00200220_11302#LTR/Gypsy	4		Os5_06_2L#LTR/Gypsy	8	4
ORSgTERT00200262_11334#LTR/Gypsy	1		Os5_08_1L#LTR/Gypsy	93	9
ORSgTERT00200318_11336#LTR/Gypsy	1		Os5_08_2L#LTR/Gypsy	45	2
ORSgTERT00200449#LTR/Gypsy	2		Os5_09_2L#LTR/Gypsy	5	
ORSgTERT00200575_11303#LTR/Gypsy	1		Os5_14_1L#LTR/Gypsy	1	
ORSgTERT00200592_11351#LTR/Gypsy	1		Os6_02_2L#LTR/Gypsy	20	3
ORSgTERT00200695_11321#LTR/Gypsy	3		Os6_04_1L#LTR/Gypsy	47	
ORSgTERT00200766#LTR/Gypsy	1		Os6_10_1L#LTR/Gypsy	14	3
ORSgTERT00200773_11303#LTR/Gypsy	1		Os6_11_1L#LTR/Gypsy	3	
ORSgTERT00200836_11306#LTR/Gypsy	1		Os6_12_1B#LTR/Gypsy	3	
ORSgTERT00200857_11303#LTR/Gypsy	2		Os6_13_1L#LTR/Gypsy	74	1
ORSgTERT00200888_11269#LTR/Gypsy	1		Os6_15_2L#LTR/Gypsy	7	1
ORSgTERT00200979_11311#LTR/Gypsy	2		Os7_03_1L#LTR/Gypsy	17	
ORSgTERT00201056_11302#LTR/Gypsy	2		Os7_05_3L#LTR/Gypsy	3	
ORSgTERT00201091_11323#LTR/Gypsy	1		Os7_06_2L#LTR/Gypsy	7	2
ORSgTERT00201114_11269#LTR/Gypsy	1		Os7_08_1L#LTR/Gypsy	42	1
ORSgTERT00201131_11305#LTR/Gypsy	1		Os7_08_2L#LTR/Gypsy	31	
ORSgTERT00201155_11345#LTR/Gypsy	2		Os8_01_6L#LTR/Gypsy	2	
ORSgTERT00201181_11316#LTR/Gypsy	1		Os8_02_1L_WD#LTR/Gypsy	2	
ORSgTERT00201216_11284#LTR/Gypsy	1		Os8_03_1L#LTR/Gypsy	1	
ORSgTERT00201271_11299#LTR/Gypsy	1		Os8_04_1L#LTR/Gypsy	2	

... continuation

LTR-retrotranposon	Up	Down	LTR-retrotranposon	Up	Down
ORSgTERT00201289_11296#LTR/Gypsy	2		Os8_04_2L#LTR/Gypsy	24	
ORSgTERT00201310_11297#LTR/Gypsy	4		Os8_04_3L#LTR/Gypsy	13	11
ORSgTERT00201315_11320#LTR/Gypsy	2		Os8_06_1L#LTR/Gypsy	8	1
ORSgTERT00201382_11280#LTR/Gypsy	2		Os8_07_2L#LTR/Gypsy	16	
ORSgTERTOOT00007_12836#LTR/Gypsy	1		Os8_08_1L#LTR/Gypsy	4	
ORSgTERTOOT00009_12852#LTR/Gypsy	1		Os8_10_1L#LTR/Gypsy	26	10
ORSgTERTOOT00012_12819#LTR/Gypsy	4		Os9_01_2L#LTR/Gypsy	5	
ORSgTERTOOT00022_12818#LTR/Gypsy	3		Os9_05_1L_A#LTR/Gypsy	5	
ORSgTERTOOT00024_12647#LTR/Gypsy	1		Os9_05_2L#LTR/Gypsy	1	
ORSgTERTOOT00043_8909#LTR/Gypsy		1	Os9_05_4L_WD#LTR/Gypsy	3	
ORSgTERTOOT00065_12861#LTR/Gypsy	2		Osr26_AP001111-0#LTR/Gypsy	99	
ORSgTERTOOT00073_12806#LTR/Gypsy	1		Osr27_AP000399-0#LTR/Gypsy	7	
ORSgTERTOOT00090_8889#LTR/Gypsy	10	3	Osr28_AP002539-0#LTR/Gypsy	2	1
ORSgTERTOOT00095_12922#LTR/Gypsy	2		Osr30_AC078891-0#LTR/Gypsy	26	1
ORSgTERTOOT00100_8959#LTR/Gypsy	1	1	osr30_AP005618-1hdnm#LTR/Gypsy	29	
ORSiTERT00200072#LTR/Gypsy	2		Osr33_AP002864-0#LTR/Gypsy	25	1
ORSiTERT00200074#LTR/Gypsy	4		Osr40_AC020666-0#LTR/Gypsy	3	1
ORSiTERT00200078#LTR/Gypsy	1		osr40_AP005618-1#LTR/Gypsy	9	1
ORSiTERT00200080#LTR/Gypsy	23	2	Osr41_AP003631-0#LTR/Gypsy	21	
ORSiTERT00200081#LTR/Gypsy	4		park_24K23-1hdnm#LTR/Gypsy	8	2
ORSiTERTOOT00003#LTR/Gypsy	4		retro_P0698G03-2#LTR/Gypsy	2	
ORSiTERTOOT00017#LTR/Gypsy	2		RETRO2_I#LTR/Gypsy	1	
ORSiTERTOOT00018#LTR/Gypsy	1		RETROSAT2LTRA#LTR/Gypsy	12	
ORSiTETNOOT00087#LTR/Gypsy	4		RETROSAT4_I#LTR/Gypsy	1	
Os1_06_1L#LTR/Gypsy	2		RETROSAT4_LTR#LTR/Gypsy	11	
Os1_08_1L_WD#LTR/Gypsy	1		RETROSAT5_I#LTR/Gypsy	1	1
Os1_11_1L#LTR/Gypsy	10	3	RETROSAT5_LTR#LTR/Gypsy	65	
Os1_13_1L#LTR/Gypsy	49		RETROSAT6_LTR#LTR/Gypsy	2	
Os1_13_2L#LTR/Gypsy	4		RETROSOR2_I#LTR/Gypsy	8	
Os1_16_1L#LTR/Gypsy	17	1	RETROSOR2_LTR#LTR/Gypsy	1	
Os1_22_1L#LTR/Gypsy	44	3	rire2#LTR/Gypsy	4	
Os11_04_1L#LTR/Gypsy	5		rire3_ac022352-0#LTR/Gypsy	8	2
Os11_05_1L#LTR/Gypsy	81	3	RIRE3_LTR#LTR/Gypsy	4	1
Os11_08_1L#LTR/Gypsy	7		rire3_P0698G03-1#LTR/Gypsy	16	7
Os11_09_4L#LTR/Gypsy	4		RIRE3A_LTR#LTR/Gypsy	2	
Os11_11_1L_WD#LTR/Gypsy	15		rire7#LTR/Gypsy	2	
Os11_12_1L#LTR/Gypsy	14	1	rire8a#LTR/Gypsy		2
Os11_14_2L#LTR/Gypsy	8		RIRE8C_LTR#LTR/Gypsy	2	
Os11_14_3L#LTR/Gypsy	21	2	RIREX_LTR#LTR/Gypsy	2	

... continuation

LTR-retrotranposon	Up	Down	LTR-retrotranposon	Up	Down
Os12_03_4L_WD#LTR/Gypsy	2		SZ-14_LTR#LTR/Gypsy	2	
Os12_04_2L#LTR/Gypsy	7		SZ-22#LTR/Gypsy	11	
Os12_05_1L#LTR/Gypsy	4	1	SZ-31_LTR#LTR/Gypsy	2	
Os12_06_2L#LTR/Gypsy	15		SZ-33_LTR#LTR/Gypsy	6	
Os12_07_1L#LTR/Gypsy	2		SZ-35_LTR#LTR/Gypsy	23	
Os12_08_1L#LTR/Gypsy	18	2	SZ-38#LTR/Gypsy	39	
Os12_09_4L#LTR/Gypsy	45	3	SZ-4#LTR/Gypsy	1	
Os12_10_1L#LTR/Gypsy	7	1	SZ-43_LTR#LTR/Gypsy	51	
Os12_10_2L#LTR/Gypsy	7	1	SZ-46LTR#LTR/Gypsy	28	
Os12_11_2L#LTR/Gypsy	31	1	SZ-50#LTR/Gypsy	5	
Os12_14_2L#LTR/Gypsy	16	1	SZ-52#LTR/Gypsy		3
Os2_01_2L#LTR/Gypsy	2		SZ-52_int#LTR/Gypsy	1	
Os2_08_3L#LTR/Gypsy	1		SZ-53#LTR/Gypsy	1	
Os2_11_1L#LTR/Gypsy		1	SZ-56#LTR/Gypsy	1	
Os2_12_1L#LTR/Gypsy	55	4	SZ-63#LTR/Gypsy	37	
Os2_14_2L#LTR/Gypsy	17	1	SZ-64B_I#LTR/Gypsy	11	
Os3_08_1L#LTR/Gypsy	3	1	SZ-66LTR#LTR/Gypsy	10	
Os3_09_1L#LTR/Gypsy	26	1	SZ-7_LTR#LTR/Gypsy	3	2
Os3_10_1L_WD#LTR/Gypsy	44	2	SZ-7A_I#LTR/Gypsy	1	1
Os3_12_1L#LTR/Gypsy	1		SZ-8#LTR/Gypsy	1	
Os3S_13L#LTR/Gypsy	3		TRUNCATOR#LTR/Gypsy	2	
Os3S_15L#LTR/Gypsy	6		TRUNCATOR2_OS#LTR/Gypsy	28	
Os3S_17L#LTR/Gypsy	4		Zm9L_97L#LTR/Gypsy	1	
Os3S_19L#LTR/Gypsy	3		ZRSiTERTOOT00132#LTR/Gypsy	1	
Os3S_1L#LTR/Gypsy	10				

Table 4.5 Number of copies of LTR retrotransposons *Ty1/Copia* class up-regulated (up) and down-regulated (down) in leaves of 18-day-old rice seedlings (*Oryza sativa* ssp. *japonica* cv. Nipponbare) after four days of iron excess exposure. The copies are located in differents positions of the same or different chromosomes.

LTR-retrotranposon	Up	Down	LTR-retrotranposon	Up	Down
COPI1_I#LTR/Copia	5		Os3S_6L#LTR/Copia	4	
COPI1_LTR#LTR/Copia	28		Os5_10_1L#LTR/Copia	1	
COPIA1-I_OS#LTR/Copia	5		Os5_13_1L#LTR/Copia	1	
COPIA1-LTR_OS#LTR/Copia	35	1	Os6_08_2L#LTR/Copia	71	1
COPIA3-I_OS#LTR/Copia	3	3	Os6_15_1L#LTR/Copia		1
COPIA3-LTR_OS#LTR/Copia	1		Os7_13_1L#LTR/Copia	8	7

... continuation

LTR-retrotranposon	Up	Down	LTR-retrotranposon	Up	Down
COPIO_I#LTR/Copia	5		osr02_AP005250-1#LTR/Copia	1	
COPIO_LTR#LTR/Copia	6		Osr06_AP001366-0#LTR/Copia	2	
CPR1_I#LTR/Copia	1	1	Osr07_AP002538-0#LTR/Copia	2	1
CPR1_LTR#LTR/Copia	2		Osr08_AC021891-0#LTR/Copia	24	2
CPSC4B_I#LTR/Copia	2		Osr12_AC073166-0#LTR/Copia	1	
Hopscotch_I#LTR/Copia	3		Osr14_AC069324-0#LTR/Copia	30	
ORSgTERT00100133_6426#LTR/Copia	4		Osr15_AP002867-0#LTR/Copia	4	5
ORSgTERT00100310_6470#LTR/Copia	2		Osr19_AC069300-0#LTR/Copia	2	
ORSgTERT00100310_6470#LTR/Copia	8		Osr24_AC016781-0part#LTR/Copia	3	
ORSgTERT00100416_6434#LTR/Copia	1		Retrofit4_I#LTR/Copia	2	
ORSgTERT00100522_6470#LTR/Copia	1		Retrofit6_I#LTR/Copia	1	
ORSgTERT00100667_6393#LTR/Copia	1	2	Retrofit7_I#LTR/Copia	1	
ORSiTERT00100063#LTR/Copia	2	1	RIRE5-LTR_OS#LTR/Copia	14	
ORSiTERT00100068#LTR/Copia	22		RN107_I#LTR/Copia		1
ORSiTERTOOT00014#LTR/Copia	9		SC-1#LTR/Copia	2	1
Os1_06_2L#LTR/Copia	6		SC-4#LTR/Copia	1	1
Os11_07_2L#LTR/Copia		4	SC-5#LTR/Copia	5	
Os12_08_2L#LTR/Copia	2		SC-7#LTR/Copia	2	
Os12_09_2L#LTR/Copia	3		SC-9#LTR/Copia	1	
Os12_09_3L#LTR/Copia	5		SZ-10old_LTR#LTR/Copia	1	
Os12_14_1L#LTR/Copia	7		SZ-25_LTR#LTR/Copia	4	
Os2_03_1L#LTR/Copia	12	3	SZ-30#LTR/Copia	7	1
Os2_05_2L#LTR/Copia	3		SZ-37#LTR/Copia	24	
Os2_08_4L#LTR/Copia	16	1	SZ-5_LTR#LTR/Copia	1	
Os2_14_1L#LTR/Copia	4		SZ-55#LTR/Copia	1	1
Os3_04_1L#LTR/Copia	1		SZ-6_int#LTR/Copia		1
Os3_13_1L#LTR/Copia	32	4	TOS17#LTR/Copia	1	
Os3S_20L#LTR/Copia	3		Zm1S_136L#LTR/Copia	1	
Os3S_21L#LTR/Copia	1		ZMCopia1_I#LTR/Copia	1	
Os3S_2L#LTR/Copia	1	4			

4.9 Co-Transcription of LTR Retrotransposons and Genes

They were identified sixteen transposable elements that are located at a distance lower than 1000 bp (Table 4.6 and Figure 4.12 A-E). Two occurrences that in which both up-regulated retrotransposon and gene present the DNA sequences overlapped and have the same sense of transcription, for example the putative co-transcription is present in the pair 5 (Table 4.6 and Figure 4.12 A) where the LTR retrotransposon Osr26_AP001111-0#LTR/Gypsy and ferric reductase-like transmembrane gene (Os04g0578600) that have the same sense of transcription and the retrotransposon sequence start in the 49 pb end of gene 3'UTR. Another putative co-transcription is the pair 15, where the gene Os12g0467700 (ATPase, AAA-type) and the retrotransposon ORSgTERT00201310_11297#LTR/Gypsy (Table 4.6 and Figure 4.12 E) where the start of retrotransposon DNA sequence is in the 13 bp end of 5'UTR of gene.

Another eight occurrences where LTR retrotransposon and gene have the same sense of transcription (plus). Five occurrences where they still have the same transcription sense (minus) and one occurrence where they have opposite senses, i.e., for the gene Os06g0706600 (Wall-associated kinase 3) (minus) and the LTR retrotransposon Os6_08_2L#LTR/Copia (plus), these two have a distance of 146 base pairs, which may indicate that the binding site for transcription factor complexes that active the gene can activate the LTR retrotransposon.

One of the most direct influences of transposable elements on the host genome is their role in modulating the structure and expression of host genes. After discovery that long terminal repeats (integral parts of some retroelements) carry promoter and enhancer motifs it became clear that integration of such elements in proximity of a host gene must have an influence on this gene expression (Sverdlov, 1998; Thornburg et al., 2006)

White et al. (1994) performed the characterization of a plant retrotransposon, Hopscotch and used this element in computer-based sequence similarity searches revealing that many normal plant genes have the remnants of *copia-like* retrotransposons in their upstream and downstream flanking regions. These results provide evidence that retroelements have the potential to be involved in the evolution of plant gene structure and expression by supplying genes with regulatory sequences and facilitating gene duplication. Furthermore, despite the fact that copia-like retrotransposons have been found in insects and fish, no element sequences were found in the flanking regions of normal animal genes.

Several lines of evidence suggest that some of the retrotransposon-like sequences identified in this study may influence the expression of adjacent genes (White et al., 1994). The retrotransposon-like sequences in the maize polygalacturonase (PG) genes contain sequence motifs that are common among genes expressed during pollen development (Allen and Lonsdale, 1993). In addition, a 501-bp fragment containing a positive regulatory region of a tomato gene expressed during pollen development (LAT59) (Twell et al., 1991) is composed entirely of a retrotransposon-like sequence.

Thornburg et al. (2006) scanned TE sequences located in promoter regions of all annotated genes in the human genome for their content in potential transcription regulating signals, and verified that all investigated signals are likely to be over-represented in at least one TE class - SINE, which shows that TEs have an important potential to contribute to pre-transcriptional gene regulation, especially by moving transcriptional signals within the genome and thus potentially leading to new gene expression patterns. They also found that some TE classes are more likely than others to carry transcription regulating signals, which can explain why they have different retention rates in regions neighboring genes.

4.10 Expression of LTR Retrotransposon Flanking Regions

Regarding expression profile of LTR retrotransposon flanking region, 81 retrotransposons that have some (upstream or downstream flanking region differentially expressed considering the sense of transcription of LTR retrotransposon) (Table 4.7), of which 44 have the flanking region downstream of final nucleotide of LTR retrotransposon sequence and 37 have the flanking region in the upstream of the first nucleotide of LTR retrotransposon sequence. In addition, the LTR retrotransposons BAJIE_LTR#LTR/Gypsy have both, upstream and downstream flanking regions up-regulated (Table 4.7).

The retrotransposon-like sequences contain identified *cis*-regulatory elements (White et al., 1994). Although in plants only a few reports do exist, in animal models, various examples can be found. Four examples of ancient retroviral insertions that provide regulatory sequences to adjacent genes have been previously described. The mouse sex-limited protein gene is expressed in the presence of androgen due to a hormone-responsive enhancer in the LTR of an endogenous provirus (Stavenhagen and Robins, 1988). In humans, an upstream endogenous retroviral

insertion has been found to be responsible for parotid-gland tissue specificity of the salivary amylase genes (Ting et al., 1992). Also, the rat oncomodulin gene and the mouse LAP-promoted placental gene are under the control of promoters in solo LTRs of rodent intracisternal A particles (IAPs) (Banville and Boie, 1989 and Chang-yeh et al., 1991).

In the *D. melanogaster* genome (Cutter et al., 2004) hypothesize that retrotransposons located in an intron are more often oriented in the opposite direction to that of the host gene and these orientation biases are stronger for genes with highly biased codon usage, probably reflecting the ability of such loci to respond to weak positive or negative selection. The leading hypothesis for selection against transposable elements in the coding orientation proposes that transcription termination poly(A) signal motifs within retroelements interfere with normal gene transcription. However, after accounting for differences in base composition between the strands, they found no evidence for global selection against spurious transcription termination signals in introns. Therefore it can be concluded that premature termination of host gene transcription due to the presence of poly(A) signal motifs in retroelements might only partially explain strand-specific detrimental effects in the *D. melanogaster* genome.

Table 4.6. Distance between genes and LTR retrotransposons, expression (log_2FC) in leaves of 18-day-old rice seedlings (*Oryza sativa* ssp. *japonica* cv. Nipponbare) after four days of iron excess exposure, pair code (pair), p-value, identification, position at chromosome and sense of transcription. Annotation according RAP-DB (build 5).

Pair	Log_2FC	P-value	Identification	Description	Chr.	Start	End	Sense	Distance
1	1.27	0	Os01g0559600	C13 endopeptidase NP1 precursor	chr01	22861073	22865586	+	
	1.1	0	Os4_12_1L_WD#LTR/Gypsy	LTR retrotransposon	chr01	22865895	22867072	+	309
2	1.14	0	Pawepe_AL662963-0#LTR	LTR retrotransposon	chr01	32720465	32721193	+	
	1.54	0.01	Os01g0742200	Elongation factor EF-2	chr01	32722092	32726861	+	899
3	1.07	0.03	Os01g0803600	Cytochrome P450	chr01	35804362	35806059	+	
	1.07	0	ORSiTETNOOT00088#DNA		chr01	35806589	35810438	+	530
4	2.1	0.09	Os01g0947000	Similar to Beta-1,3-glucanase	chr01	43397984	43400378	+	
	1.14	0	SZ-35_LTR#LTR/Gypsy		chr01	43400560	43404455	+	182
5	1.11	0.04	Osr26_AP001111-0#LTR/Gypsy	LTR retrotransposon	chr04	29666781	29678091	-	
	1.25	0.01	Os04g0578600	Ferric reductase-like transmembrane	chr04	29678042	29680811	-	-49
6	1.15	0	Os04g0471700	WRKY transcription factor 35	chr04	24078999	24086336	-	
	1.04	0	Pawepe_AL662963-0#LTR		chr04	24087085	24087842	-	749
7	1.31	0.01	Os06g0706600	Wall-associated kinase 3	chr06	30727304	30732923	-	
	1.25	0.01	Os6_08_2L#LTR/Copia	LTR retrotransposon	chr06	30733069	30738753	+	146
8	1.22	0	Os08g0201700	Protein kinase activity	chr08	5888204	5893292	+	
	1.09	0.01	Os4_01_1L#LTR/Gypsy	LTR retrotransposon	chr08	5893307	5904589	+	15
9	1.19	0	ORSiTETN00200012#DNA/En-Spm		chr08	8820762	8835743	+	
	1.08	0	Os08g0244500	Beta-1,3-glucanase-like protein	chr08	8836259	8838358	+	516
10	1.34	0	SZ-63#LTR/Gypsy	LTR retrotransposon	chr08	8974281	8976096	-	
	1.46	0	Os08g0246950	Heat-shock protein	chr08	8976540	8977719	-	444
11	1.03	0.02	Os2_05_3L#LTR	LTR retrotransposon	chr11	6039701	6040480	-	
	1	0	Os11g0216000	Pyruvate kinase family protein	chr11	6041261	6047305	+	781
12	1.02	0.04	Os11g0675200	NB-ARC domain containing protein	chr11	29481820	29484903	+	
	2.11	0.04	osr14_AP005618-1solohdnm#LTR	LTR retrotransposon	chr11	29485770	29489132	+	867
13	1.45	0	Os12g0263800	Aspartic proteinase oryzasin 1	chr12	9307031	9325635	-	
	1.5	0	COPI1_LTR#LTR/Copia	LTR retrotransposon	chr12	9325834	9326147	-	199
14	1.76	0	Os12_06_3L#LTR	LTR retrotransposon	chr12	10419338	10424194	-	
	1.02	0.02	Os12g0278700	Similar to cystinosin.	chr12	10425185	10433345	-	991
15	1.13	0	Os12g0467700	ATPase, AAA-type	chr12	16773266	16775190	+	
	1.07	0.01	ORSgTERT00201310_11297#LTR/Gypsy	LTR retrotransposon	chr12	16775177	16779563	-	-13
16	1.05	0.04	Os2_14_1L#LTR/Copia	LTR retrotransposon	chr12	23655311	23660027	+	
	2.43	0	Os12g0571000	Metallothionein-like protein type 1	chr12	23660803	23661708	+	776

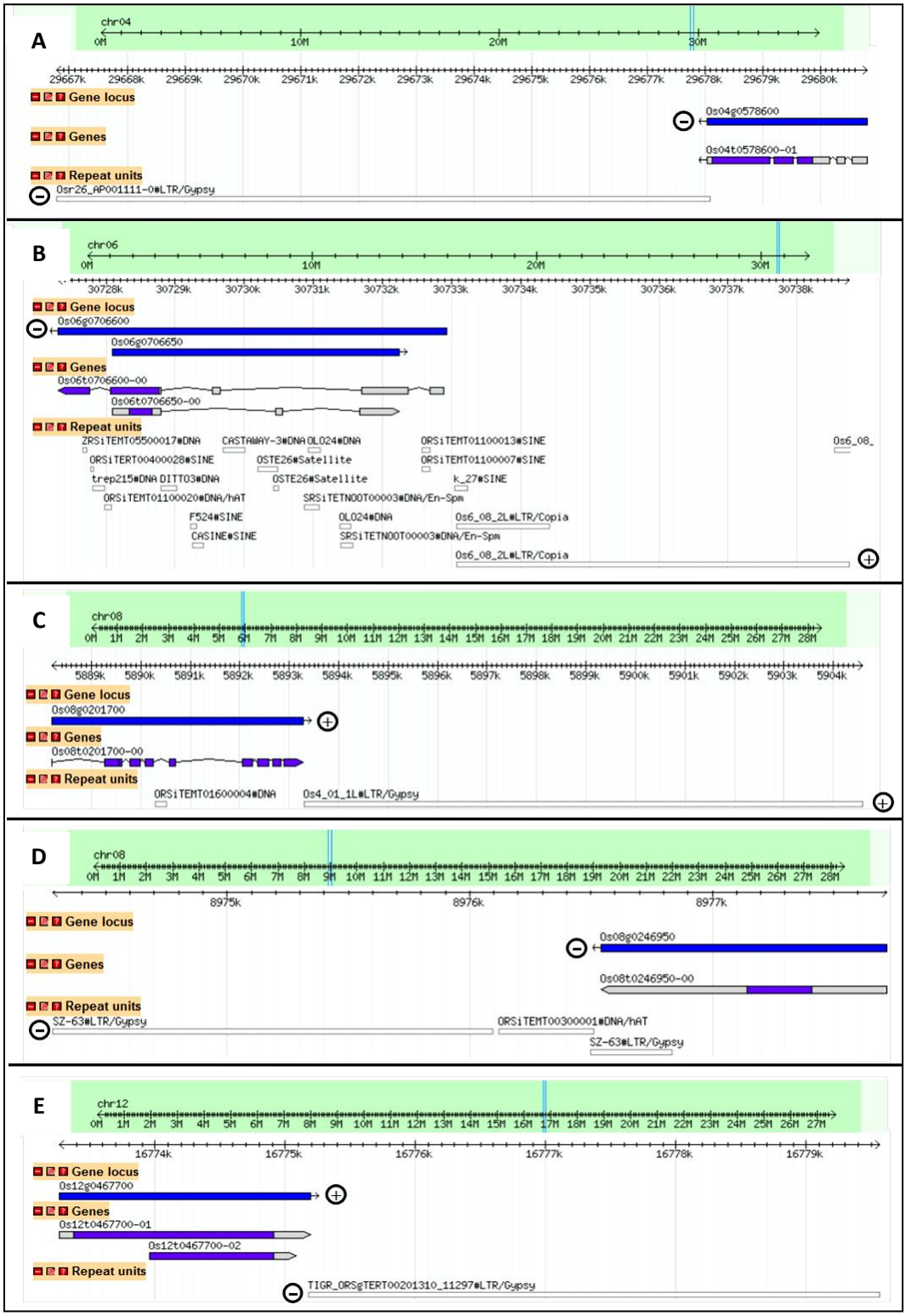

Figure 4.12 Representation of genes and LTR retrotransposons that have a distance < 1000 pb and are up-regulated in leaves of 18-day-old rice seedlings (*Oryza sativa* ssp. *japonica* cv. Nipponbare) after four days of iron excess exposure. Images generated by GBrowse Annotation according RAP-DB (build 5). According with pair described in table 4.6. A) Pair 5 B) Pair 7 C) Pair 8 D) Pair 10 E) Pair 15.

Table 4.7. Expression of flanking regions and distance of genes or LTR retrotransposons, expression level (log2FC) in leaves of 18-day-old rice seedlings (*Oryza sativa* ssp. *japonica* cv. Nipponbare) after four days of iron excess exposure, position related to position of LTR retrotransposon (Downstream, Upstream or Both), p-value, identification, position at chromosome (Chr, Stard and End) and sense of transcription. Annotation according RAP-DB (build 5).

Position	Log_2FC	p-value	Chr	Start	End		Distance	Identification
	1.22	0.01	1	4574476	4574535	-		Flanking region
Both	1.13	0	1	4574644	4575370	+	109	BAJIE_LTR#LTR/Gypsy
	1.23	0	1	4575462	4575521	-	92	Flanking region
	1.19	0	1	21331358	21331417	-		Flanking region
Downst.	1.29	0.02	1	21331917	21334777	-	500	SZ-38#LTR/Gypsy
	1.9	0	1	27974290	27974349	-		Flanking region
Downst.	1.9	0.03	1	27975027	27976264	-	678	SZ-30#LTR/Copia
	1.05	0	1	28485665	28486239	+		SZ-33_LTR#LTR/Gypsy
Downst.	1.73	0	1	28486450	28486509	-	211	Flanking region
	1.22	0	1	23028219	23032097	-		Os5_11_1L#LTR
Upstr.	1.46	0	1	23032441	23032500	-	344	Flanking region
	1.98	0.01	1	23377114	23377173	-		Flanking region
Upstr.	1.76	0	1	23377596	23381364	+	423	Os3S_22L#LTR/Gypsy
	1.17	0.01	1	24031598	24043058	+		Os3_09_1L#LTR/Gypsy
Downst.	1.24	0	1	24043637	24043696	-	579	Flanking region
	-1.59	0.04	1	22495791	22495850	-		Flanking region
Downst.	1.94	0.01	1	22496219	22497704	-	369	Os1_13_1L#LTR/Gypsy
	-1.03	0.04	2	11110630	11110689	-		Flanking region
Downst.	1.16	0.04	2	11111189	11115326	-	500	ORSgTERT00100310_6470#LTR/Copia
	-1.2	0.04	2	22636615	22636674	-		Flanking region
Downst.	1.06	0	2	22637372	22640454	-	698	Os02g0570700
	1.99	0	2	25075328	25075387	-		Flanking region
Upstr.	1.82	0.01	2	25075774	25076484	+	387	Os2_05_3L#LTR
	1.14	0	2	28687976	28688702	-		BAJIE_LTR#LTR/Gypsy
Downst.	1.59	0	2	28688820	28688879	-	118	Flanking region
	1.6	0	3	9444323	9445054	-		BAJIE_LTR#LTR/Gypsy
Upstr.	1.12	0	3	9445652	9445711	-	598	Flanking region
	1.33	0	3	22914757	22917861	+		Osr30_AC078891-0#LTR/Gypsy
Downst.	1.23	0	3	22918797	22918856	-	936	Flanking region
	1.62	0	3	26264525	26268945	-		osr37_AP005618-1hdnm#LTR
Upstr.	1.21	0	3	26268981	26269040	-	36	Flanking region
	1.39	0	4	3148846	3148905	-		Flanking region
Upstr.	1.2	0.02	4	3149049	3160730	+	144	Os5_08_1L#LTR/Gypsy
	1.08	0.02	4	6612607	6612666	-		Flanking region
Upstr.	1.01	0.04	4	6612669	6615641	+	3	Os12_09_4L#LTR/Gypsy
	1.14	0	4	8666797	8678835	+		Os12_09_4L#LTR/Gypsy
Downst.	1.4	0	4	8679770	8679829	-	935	Flanking region
	1.36	0	4	10329204	10329263	-		Flanking region
Downst.	1.32	0	4	10329666	10330618	-	403	Os2_08_1L#LTR
	2.19	0.01	4	10856210	10856269	-		Flanking region
Upstr.	1.11	0	4	10857159	10866539	+	890	Osr26_AP001111-0#LTR/Gypsy
	1.44	0	4	10866540	10869351	-	1	Os7_08_1L#LTR/Gypsy

...continuation

Position	Log_2FC	p-value	Chr	Start	End		Distance	Identification
Upstr.	1.38	0.01	4	14012753	14019183	-		Os6_08_2L#LTR/Copia
	2.48	0	4	14019574	14019633	-	391	Flanking region
Downst.	1.98	0	4	14661130	14666548	+		Os8_10_1L#LTR/Gypsy
	1.35	0.01	4	14666867	14666926	-	319	Flanking region
Upstr.	1.26	0	4	34409233	34413821	-		Os11_05_1L#LTR/Gypsy
	1	0	4	34414660	34414719	-	839	Flanking region
Downst.	1.38	0	5	8735204	8735263	-		Flanking region
	1.68	0	5	8735439	8737553	-	176	Os5_13_2L#Retroelement
Downst.	1.95	0	5	10300905	10306721	+		Os1_13_1L#LTR/Gypsy
	1.02	0.01	5	10307434	10307493	-	713	Flanking region
Upstr.	1.15	0	5	10867658	10873994	-		Os11_01_2L#Retroelement
	1.81	0.01	5	10874124	10874183	-	130	Flanking region
Downst.	1.7	e-05	5	13546456	13547148	+		pawepe_AP005250-1solo#Other
	1.22	0	5	13547284	13547343	-	136	Flanking region
Downst.	1.33	0	5	14661502	14665210	+		Os11_08_2L#LTR
	1.1	0.01	5	14665484	14665543	-	274	Flanking region
Upstr.	2.36	0	6	5471811	5472071	-		Osr14_AC069324-0#LTR/Copia
	1.23	0.01	6	5472884	5472943	-	813	Flanking region
Downst.	1.27	0	6	8430120	8430179	-		Flanking region
	1.01	0	6	8430815	8431518	+	636	Os11_08_2L#LTR
Downst.	-1.19	0.05	6	8623041	8623100	-		Flanking region
	1.03	0	6	8623616	8626531	-	516	Os11_05_1L#LTR/Gypsy
Upstr.	1.5	0	6	9888354	9894768	-		Os6_08_2L#LTR/Copia
	1.11	0.01	6	9894873	9894932	-	105	Flanking region
Downst.	1.1	0	6	14433934	14437646	+		Os5_12_1L#Retroelement
	1.04	0.03	6	14437738	14437797	-	92	Flanking region
	1.13	0.01	6	14437744	14437803	-	-53	Flanking region
Downst.	2.09	0.02	6	21665048	21668422	-		SZ-46LTR#LTR/Gypsy
	1.13	0.01	6	21668725	21668784	-	303	Flanking region
Upstr.	1.08	0	6	22590977	22591746	+		SZ-22#LTR/Gypsy
	1.35	0	6	22592364	22592423	-	618	Flanking region
Downst.	1.55	0.01	6	31292019	31292078	-		Flanking region
	1.3	0	6	31292411	31292885	-	333	Os2_14_1L#LTR/Copia
Upstr.	1.06	0	7	3197811	3198093	-		COPI1_LTR#LTR/Copia
	-1.01	0.04	7	3198225	3198284	-	132	Flanking region
Upstr.	1.52	0.01	7	11220290	11220349	-		Flanking region
	1.26	0	7	11220471	11221397	+	122	Os12_06_4L_WD#LTR
Upstr.	1.1	0.04	7	11435199	11435258	-		Flanking region
	1.23	0	7	11435480	11442469	+	222	Os7_09_1L#Retroelement
Downst.	1.23	0	7	13117310	13120380	+		SZ-43_LTR#LTR/Gypsy
	1.26	0.01	7	13120737	13120796	-	357	Flanking region
Downst.	1.04	0.02	7	29170022	29170081	-		Flanking region
	1.08	0	7	29170761	29182056	-	680	Os12_10_2L#LTR/Gypsy
Upstr.	1.55	0	8	1419507	1419566	-		Flanking region
	1.37	0	8	1419869	1426282	+	303	Os12_03_3L#LTR/Gypsy

...continuation

Position	Log_2FC	p-value	Chr	Start	End		Distance	Identification
Downst.	1.35	0.04	8	2694227	2694286	-		Flanking region
	1.22	0.01	8	2694601	2697836	-	315	Osr30_AC078891-0#LTR/Gypsy
Downst.	1.06	0	8	12144556	12146660	+		Os1_16_1L#LTR/Gypsy
	1.07	0.02	8	12147626	12147685	-	966	Flanking region
Upstr.	1.19	0.03	8	13211919	13211978	-		Flanking region
	1.32	0.01	8	13212095	13213877	+	117	Os5_05_3L#LTR
Downst.	1.06	0	8	14557707	14558670	+		RIRE5-LTR_OS#LTR/Copia
	1.04	0.01	8	14558888	14558947	-	218	Flanking region
Downst.	-1	0.03	8	17187446	17187505	-		Flanking region
	1.3	0.01	8	17187994	17197171	-	489	Os3_13_1L#LTR/Copia
Upstr.	1.73	0	9	3933865	3936992	-		Os5_08_2L#LTR/Gypsy
	1.54	0	9	3937239	3937298	-	247	Flanking region
	1.19	0.01	9	3937707	3937766	-	409	Flanking region
Upstr.	1.26	0	9	7138377	7138436	-		Flanking region
	1.57	0	9	7139141	7140660	+	705	Os11_08_2L#LTR
Upstr.	1.26	0	9	7138377	7138436	-		Flanking region
	1.57	0	9	7139141	7140660	+	705	Os11_08_2L#LTR
Downst.	2.71	0	9	8911509	8911568	-		Flanking region
	1.36	0.02	9	8912210	8912908	-	642	Os11_08_2L#LTR
Upstr.	1.23	0.01	10	4995566	4998415	-		Os5_08_1L#LTR/Gypsy
	1.34	0	10	4998639	4998698	-	224	Flanking region
Upstr.	1.45	0.01	10	7152445	7154291	-		osr30_AP005618-1hdnm#LTR/Gypsy
	-1.13	0.04	10	7154950	7155009	-	659	Flanking region
Upstr.	1.08	0	10	11002141	11002554	-		Os2_06_1L_UI#LTR
	1.12	0	10	11002982	11003041	-	428	Flanking region
Upstr.	1.42	0	10	13446818	13447495	-		Os9_04_1L#LTR
	1.49	0	10	13447895	13447954	-	400	Flanking region
Upstr.	1.2	0.01	10	14954801	14954860	-		Flanking region
	1.04	0.01	10	14955444	14955824	+	584	Os3S_6L#LTR/Copia
Upstr.	1.51	0.01	10	15287695	15287754	-		Flanking region
	1.04	0.01	10	15287834	15289331	+	80	SZ-37#LTR/Copia
Downst.	1.08	0.02	10	16054659	16054718	-		Flanking region
	1.17	0.01	10	16055312	16067549	-	594	Os6_10_1L#LTR/Gypsy
Downst.	1.04	0	10	19210241	19211321	+		Os4_03_4L#LTR/Gypsy
	1.02	0.01	10	19212261	19212320	-	940	Flanking region
Upstr.	1.46	0	10	20622933	20622992	-		Flanking region
	1.09	0	10	20623439	20631210	+	447	SZ-64B_I#LTR/Gypsy
Upstr.	1.43	0.03	11	971514	971573	-		Flanking region
	1.3	0	11	972071	973970	+	498	osr30_AP005618-1hdnm#LTR/Gypsy
Downst.	1.48	0	11	1161713	1161772	-		Flanking region
	1.36	0.02	11	1162400	1166171	-	628	Os2_06_1L_UI#LTR
Upstr.	1.06	0.01	11	2411782	2413292	-		SZ-19_LTR#LTR
	1.8	0	11	2414233	2414292	-	941	Flanking region
Downst.	1.48	0	11	4175006	4175065	-		Flanking region
	1,00	0.01	11	4175565	4179887	-	500	Os1_13_1L#LTR/Gypsy

...continuation

Position	Log_2FC	p-value	Chr	Start	End		Distance	Identification
Downst.	1.04	0.01	11	4473327	4473386	-		Flanking region
	1.14	0.02	11	4473952	4477187	-	566	Os6_08_2L#LTR/Copia
Downst.	1.06	0.02	11	17296558	17308202	+		Os6_02_2L#LTR/Gypsy
	1.14	0	11	17308682	17308741	-	480	Flanking region
Downst.	1.18	0	11	19452147	19456146	+		Os3S_14L#LTR
	1.35	0	11	19456959	19457018	-	813	Flanking region
Downst.	1.09	0	11	19630005	19630211	+		COPI1_LTR#LTR/Copia
	1.11	0.03	11	19630646	19630705	-	435	Flanking region
Downst.	1.87	0	11	20024702	20024761	-		Flanking region
	2.2	0	11	20024988	20029468	-	227	Os12_08_2L#LTR/Copia
	1.67	0	11	24412254	24412313	-		Flanking region
Downst.	1.08	0	11	24412646	24414167	-	333	ATLANTYS-LTR_OS#LTR/Gypsy
	1.39	0.01	11	25055582	25059485	-		Os9_04_1L#LTR
Upstr.	1.48	0	11	25060422	25060481	-	937	Flanking region
Downst.	1.59	0.02	11	26513835	26517671	+		SZ-35_LTR#LTR/Gypsy
	1.44	0	11	26518064	26518123	-	393	Flanking region
Upstr.	1.71	0	11	26549781	26563606	-		Os1_22_1L#LTR/Gypsy
	1.5	0	11	26563722	26563781	-	116	Flanking region
Upstr.	1.11	0	12	3699238	3699297	-		Flanking region
	1.12	0	12	3699356	3701233	+	59	RETROSAT5_LTR#LTR/Gypsy
Downst.	1.03	0.04	12	5566408	5566467	-		Flanking region
	1.21	0	12	5566527	5572724	-	60	Os6_08_2L#LTR/Copia
Upstr.	1.85	0.01	12	6557368	6557427	-		Flanking region
	1.15	0.01	12	6558078	6563511	+	651	TIGR_ORSgTERT00100133_6426#LTR/Copia
Downst.	1.04	0	12	9982842	9985243	-		Os4_02_1L#LTR
	1.02	0.01	12	9985695	9985754	-	452	Flanking region
Upstr.	1.63	0	12	10693756	10693815	-		Flanking region
	1.37	0	12	10694571	10696159	+	756	SZ-37#LTR/Copia
Downst.	1.22	0.01	12	14223742	14224901	+		Os12_06_4L_WD#LTR
	2.17	0.02	12	14225131	14225190	-	230	Flanking region
Dowstr.	1.05	0	12	15539589	15553457	-		Os3S_9L#LTR/Gypsy
	1.04	0.01	12	15554029	15554088	-	572	Flanking region
Upstr.	1.16	0	12	16076466	16076525	-		Flanking region
	1.42	0	12	16076539	16080752	+	14	Os8_07_2L#LTR/Gypsy
Downst.	2.55	0	12	17009480	17009539	-		Flanking region
	1.38	0	12	17010269	17010968	-	730	Os5_11_1L#LTR
Downst.	1.32	0	12	19051538	19051597	-		Flanking region
	1.69	0	12	19051651	19055360	-	54	Os2_06_1L_UI#LTR

CHAPTER V

GENERAL DISCUSSION

The cultivar Nipponbare is considered tolerant to excess iron. Previous reports showed that in a nutritive solution with 250 mg L^{-1} of Fe^{2+} Nipponbare was not significantly different to the cultivar Suakoko8 (iron toxicity tolerant control) regarding leaf bronzing index after 28 days of exposure to excess iron (Wan et al., 2003). In this study, 18-day-old rice seedlings (cv. Nipponbare) after four days of exposition to iron excess (7 mM or 390 mg L^{-1} of $FeSO_4.7H_2O$) absorbed more than 2x the amount of iron than the seedlings in the control condition (optimum amount of iron). This iron absorbed would be stored in ferritins and immobilized by chelation (Briat et al., 1999; Zancani et al., 2004). However, changes in gene expression were not observed for iron storage proteins. On the other hand, after four days of exposition to iron excess, a response to an oxidative burst was quite remarkable.

In this study, 18-day-old seedlings after four days of exposition to iron excess (7 mM of $FeSO_4.7H_2O$) showed symptoms, making it possible to visualize some brown spots in the leaves. Although a huge amount of up-regulated genes were found, creating some complexity in data interpretation, a large number of metabolic pathways in which changes occurred, were detected. They were observed a large number of transcription factors and kinases - from those present in the cell wall, as those who act in the nucleus and activate transcription factors - and the *in silico* analysis of up-regulated promoter region (1kbp upstream) revealed that ca. 28% of these genes are ABA-responsive indicating a cross-talk of signaling for iron toxicity.

Considering the visible presence of symptoms (browning spots), is possible to infer that iron was absorbed in excess by roots and after four days an oxidative stress was taking place in the leaves. In the Figure 5.1 is represented a schematic depiction of signaling cascade in the cell in response to iron excess with the up-regulated genes in this work. The iron excess Fe^{2+} enters in the cell, an oxidative burst in the chroloplasts and mithocondrion is verified (excessive production of reactive oxygen species - ROS production occurs) by means of increasing the Fenton Reaction (Pierre and Fontecave, 1999). Additionally, the increases in ROS and ABA are observed in the apoplast, affecting membrane and cell wall receptors, such as WAKs (wall associated kinases) and RLKs (receptor like kinase), that activate signaling cascade by phosphorilation of MAP kinases. These, in sequence, activate transcription factors responsive to stress that will recognise and and bind to specific *cis*-regulatory elements in promoter region of genes, modulating its expression. The main responsive transcription factors found in this work were *bHLH, WRKY,bZIP, HSP, ERFs, ZF, AREB2* and *MYB* that in turn activate among others,

the genes that can cope with oxidative stress and ROS signaling, such as GSTs (glutathione S-transferase), SOD (superoxide dismutase), POD (peroxidase) and GSH (gluthathione), these protein ares ROS scavengers, and contribute to redox homeostasis in cell (Figure 5.1).

Another group of up-regulated target genes verified in this work was composed of heavy metal detoxification genes, such as cytocrome P450, metalothioneins, and MATE family of tranporters and alternative oxidase (AOX 1a and 1b) that can help to reduce de ROS production in mitochondrion. The most part of up-regulated genes codify proteins that act in mitochondria or plastids, organelles that are involved in iron metabolism and ROS production.

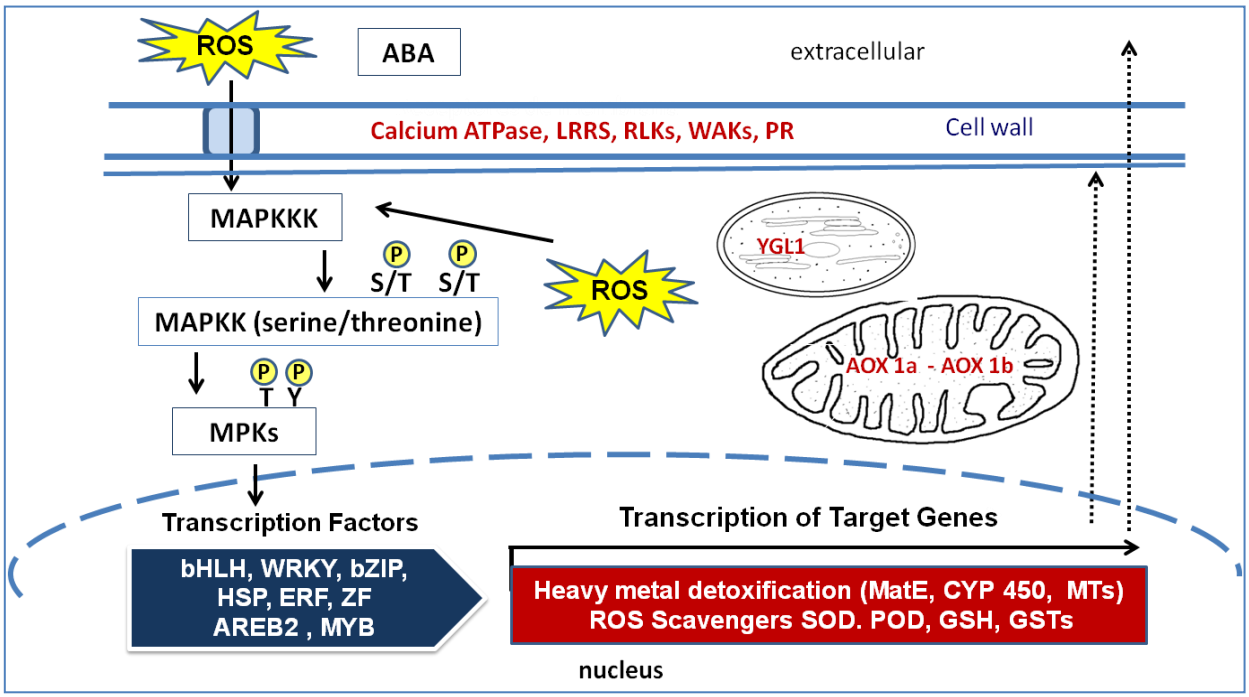

Figure 5.1 Schematic depiction of iron toxicity responsive genes (up-regulated) in leaves of 18-day-old rice seedlings after four days of exposition to iron excess: in the cell wall and cellular membrane, calcium ATPase, LRRs (leucine rich repeat), RLK (receptor-like quinase), WAK (wall associated kinases), PR1a (Pathogenesis related) receive the ROS signal and phosphorilate serine (S) and tyrosine (T) residues of MAP3K that phosphorilate tyrosine/threonime (Y) residues in MAPKs that that phosphorilate transcription factors such as WRKY, bZIP and zinc fingers (ZF) that recognize and bind to cis-regulatory elements in promoter region of stress responsive genes such as ROS scavengers, transporters and others. In mitochondria, AOX (oxidase-alternative 1a and 1b) and in chloroplast YGL1 (*Oryza sativa* yellow-green leaf1/chlorophyll synthetase) help to make detoxification of excessive ROS (reactive oxygen species) released by oxidative burst generated in mitochondria and chloroplasts. Source: Taciane Finatto, 2012.

They were observed a large activity of LTR retrotransposons in response to iron toxicity, and furthermore, they were verified that LTR retrotransposons transcription can extend to 5' and 3' flanking regions as seen in 16 situations that should up-regulated genes and flanking regions that are located at a very short distance in the same chromosome suggesting co-transcription. We also found instances in which up-regulated LTR retrotransposons are located in the 3'UTR of an upstream gene.

Sixteen transposable elements that are located at a distance lower than 1000 bp. Two occurrences in which the DNA sequences of both up-regulated retrotransposon and gene are overlapped and have the same sense of transcription, for example the putative co-transcription is the LTR retrotransposon Osr26_AP001111-0#LTR/Gypsy and ferric reductase-like transmembrane gene (Os04g0578600) that have the same sense of transcription and the retrotransposon sequence start in the 49 pb end of gene 3'UTR. Another putative co-transcription where the gene Os12g0467700 (ATPase, AAA-type) and the LTR retrotransposon ORSgTERT00201310_11297#LTR/Gypsy where the start of retrotransposon DNA sequence is in the 13 bp end of 5'UTR of gene. Another eight occurrences where LTR retrotransposon and gene have the same sense of transcription (plus). Five occurrences where they still have the same transcription sense (minus) and one occurrence where they have opposite senses, i.e., for the gene Os06g0706600 (Wall-associated kinase 3) (minus) and the LTR retrotransposon Os6_08_2L#LTR/Copia (plus), these two have a distance of 146 base pairs, which may indicate that the binding site for transcription factor complexes that active the gene can activate the LTR retrotransposon.

This study provided the identification of numerous genes and LTR transposons that are involved in the response to iron toxicity in rice, and that present a potential for future studies on genetic transformation in order to verify the function of genes in the phenotypic responses to iron toxicity in rice mutants. Also, further studies such as the validation of co-transcription LTR retrotransposons-gene and/or their flanking regions by cDNA-PCR and sequencing can comfirm this first approach.

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ANNEX

Annex 1 Function related of up-regulated genes, expression (log2FC), p-value, locus ID, and description of gene function in leaves of 18-day-old rice seedlings (*Oryza sativa* ssp. *japonica* cv. Nipponbare) after four days of iron excess exposure.

Log_2FC	P-value	Locus-ID	Description
1.04	0	Os07g0274700	(B12Dg1 protein)
1.05	0	Os04g0475600	2OG-(FeII) oxygenase
1.14	0	Os06g0255100	2OG-(FeII) oxygenase
1.02	0	Os12g0168000	5-formyltetrahydrofolate cyclo-ligase
1.01	0	Os11g0135400	60S acidic ribosomal protein P0
1.27	0	Os12g0211400	A/G-specific adenine glycosylase MutY, bacterial form
1.87	0	Os01g0963600	ABA/WDS induced protein
1.08	0	Os11g0605500	Acyl-CoA oxidase
1.11	0	Os03g0576600	Acyl-CoA-binding protein (ACBP)
1.41	0	Os12g0197400	AIG1 domain containing protein
1.2	0	Os06g0602600	Alba, DNA/RNA-binding protein
1.12	0	Os08g0109200	Alcohol dehydrogenase superfamily
1.12	0	Os02g0294700	Aldehyde dehydrogenase, conserved site
1.29	0	Os01g0580100	Alg9-like mannosyltransferase
1.44	0	Os12g0227400	Allyl alcohol dehydrogenase
1.8	0	Os05g0363100	Alpha/beta hydrolase
1.11	0	Os05g0370700	Alpha/beta hydrolase
2.06	0	Os12g0117100	Alpha/beta hydrolase fold-1
1.69	0	Os07g0162400	Alpha/beta hydrolase fold-3
3.04	0	Os07g0526600	Alpha/beta hydrolase fold-3
1.49	0	Os07g0643601	Alpha/beta hydrolase fold-3
1.28	0	Os04g0600200	Alternative oxidase 1a
1.11	0	Os04g0184100	Amidase family protein
1.01	0	Os02g0655700	Amino acid/polyamine transporter I
1.18	0	Os10g0430600	Aminotransferase, class-II, pyridoxal-phosphate
1.02	0	Os05g0317200	AMP-dependent synthetase and ligase
1.2	0	Os05g0170800	ApaG domain containing protein
1.04	0	Os07g0448800	Aquaporin
1.49	0	Os07g0587500	Armadillo-like helical
1.54	0	Os12g0538900	Armadillo-type fold
1.59	0	Os02g0120100	ATMRK serine/threonine protein kinase-like
1.12	0	Os07g0475900	ATMRK serine/threonine protein kinase-like
1.3	0	Os01g0641800	ATPase, AAA-type, core
1.02	0	Os03g0802500	ATPase, AAA-type, core
1.98	0	Os07g0192700	ATPase, AAA-type, core
1.62	0	Os11g0661400	ATPase, AAA-type, core
1.13	0	Os12g0467700	ATPase, AAA-type, core
1.84	0	Os12g0639500	ATPase, AAA-type, core
1.08	0	Os10g0412000	ATPase, P-type, K/Mg/Cd/Cu/Zn/Na/Ca/Na/H-
1.14	0	Os09g0491740	Auxin efflux carrier
1.94	0	Os09g0508100	Auxin responsive SAUR protein
1.05	0	Os02g0743400	Auxin transport protein REH1

1.48	0	Os07g0182000	Basic leucine zipper factor 1
1.71	0	Os05g0569900	B-block binding subunit of TFIIIC
1.05	0	Os02g0226801	Bet v I allergen family protein
1.32	0	Os06g0686400	Bifunctional inhibitor/plant lipid transfer protein
1.18	0	Os09g0270900	BolA-like protein
1.16	0	Os06g0726400	Branching enzyme-I precursor
1.23	0	Os01g0385400	C4-dicarboxylate transporter/malic acid transport
1.57	0	Os05g0219900	C4-dicarboxylate transporter/malic acid transport
1.15	0	Os05g0584900	C4-dicarboxylate transporter/malic acid transport
1.27	0	Os01g0835700	CCT domain containing protein
1.19	0	Os02g0534400	Cell wall invertase (EC 32126)
1.03	0	Os10g0389000	Centrin
1.06	0	Os04g0320100	Coenzyme F420 hydrogenase/dehydrogenase beta
1.55	0	Os12g0635700	Conserved hypothetical protein
1.88	0	Os06g0338700	Copper amine oxidase
1.14	0	Os09g0440700	Ctr copper transporter
1.32	0	Os06g0286228	Cupredoxin
1.03	0	Os10g0123200	Cyclin-like F-box domain containing protein
1.07	0	Os11g0208000	Cyclin-like F-box domain containing protein
1.31	0	Os11g0533800	Cyclin-like F-box domain containing protein
1.12	0	Os11g0582700	Cyclin-like F-box domain containing protein
1.23	0	Os12g0164300	Cyclin-like F-box domain containing protein
1.6	0	Os01g0803200	Cysteine proteinase inhibitor-I
1.04	0	Os04g0165700	Cysteine synthase EC 25147
1.14	0	Os01g0266800	Cystinosin/ERS1p repeat containing protein
1.15	0	Os01g0691500	Cytidylyltransferase
1.32	0	Os10g0504200	Cytochrome b561
1.74	0	Os07g0567400	Cytochrome c region
1.85	0	Os01g0561600	Cytochrome P450
1.06	0	Os01g0602500	Cytochrome P450
1.42	0	Os01g0628900	Cytochrome P450
1.12	0	Os02g0185300	Cytochrome P450
1.52	0	Os02g0187000	Cytochrome P450
1.28	0	Os02g0529800	Cytochrome P450
1.06	0	Os02g0570700	Cytochrome P450
1.64	0	Os03g0760200	Cytochrome P450
1.2	0	Os06g0501900	Cytochrome P450
1.06	0	Os07g0217600	Cytochrome P450
3.59	0	Os07g0218700	Cytochrome P450
1.14	0	Os07g0519300	Cytochrome P450
1.1	0	Os10g0139700	Cytochrome P450
1.71	0	Os10g0439700	Cytochrome P450
1.92	0	Os10g0513900	Cytochrome P450
1.69	0	Os10g0513400	Cytochrome P450
1.05	0	Os10g0515900	Cytochrome P450
1.03	0	Os10g0525200	Cytochrome P450

1.63	0	Os12g0512800	Cytochrome P450 71E1 EC 1141368
1.12	0	Os01g0184500	DEAD-like helicase, N-terminal
1.16	0	Os08g0289400	DEAD-like helicase, N-terminal
1.24	0	Os11g0533100	DEAD-like helicase, N-terminal
1.16	0	Os01g0165000	Dehydration-responsive element-binding protein 2A
1.05	0	Os07g0179400	Dephospho-CoA kinase
1.19	0	Os07g0607700	Di-trans-poly-cis-decaprenylcistransferase
1.7	0	Os05g0498300	DNA mismatch repair protein MutS, core
1.79	0	Os01g0881400	DNA repair metallo-beta-lactamase
1.19	0	Os11g0117500	DNA-binding WRKY
1.06	0	Os05g0179100	DVL family protein
1.62	0	Os02g0559800	E3 ubiquitin ligase EL5
1.59	0	Os08g0558100	EF hand domain containing protein
1.63	0	Os04g0511200	EFA27 for EF hand, abscisic acid, 27kD
1.5	0	Os01g0505600	EF-Hand type
1.62	0	Os02g0220500	Elongation factor 1-gamma
1.07	0	Os01g0610600	Endonuclease/exonuclease/phosphatase
1.06	0	Os08g0567100	ENTH/VHS domain containing protein
1.4	0	Os06g0570100	Ent-kaurene oxidase
1.07	0	Os06g0156400	Esterase, SGNH hydrolase-type, subgroup
1.94	0	Os04g0433200	Etoposide-induced 24
1.67	0	Os11g0649900	Exo70 exocyst complex subunit
1.39	0	Os10g0553600	Exostosin-like
1.1	0	Os03g0636600	Expressed protein
1.64	0	Os01g0316100	FAD dependent oxidoreductase
1.62	0	Os06g0549900	FAD linked oxidase, N-terminal
1.32	0	Os07g0187200	FAD linked oxidase, N-terminal
1.29	0	Os06g0549600	FAD-linked oxidase, FAD-binding, subdomain 2
1.21	0	Os11g0495950	FAD-linked oxidase, FAD-binding, subdomain 2
1.09	0	Os06g0226950	Fatty acid hydroxylase
1.18	0	Os08g0517500	FMN-binding split barrel
1.69	0	Os05g0407100	Four F5 protein
1.19	0	Os06g0207000	Fumble domain containing protein
1.13	0	Os01g0355600	Galactose-binding like
1.19	0	Os08g0189400	Germin-like protein precursor
1.68	0	Os07g0592000	Gibberellin regulated protein
1.81	0	Os01g0227100	Glucose/ribitol dehydrogenase
1.26	0	Os03g0685300	Glutamine amidotransferase class-I
1.08	0	Os03g0651000	Glu-tRNAGln amidotransferase, C subunit
2.17	0	Os04g0513900	Glycoside hydrolase, family 1 protein
1.04	0	Os09g0511600	Glycoside hydrolase, family 1 protein
1.09	0	Os09g0520800	Glycoside hydrolase, family 29 (alpha-L-fucosidase)
1.3	0	Os12g0406100	Glycoside hydrolase, family 43 protein
1.26	0	Os01g0773600	Glycoside hydrolase, family 47 protein
1.19	0	Os06g0602800	Glycosyl transferase, family 14 protein
1.27	0	Os01g0653200	Glycosyl transferase, group 1

1.31	0	Os01g0956200	Glycosyltransferase AER61, uncharacterized
1.03	0	Os11g0575500	Glycosyltransferase AER61, uncharacterized
1.4	0	Os04g0538900	Glyoxalase/bleomycin resistance protein/dioxygenase
1.5	0	Os05g0171900	Glyoxalase/bleomycin resistance protein/dioxygenase
1.14	0	Os03g0799700	GTP1/OBG subdomain containing protein
1.24	0	Os05g0333200	Guanine nucleotide-binding protein alpha-1 subunit
1.07	0	Os02g0227000	HAD superfamily hydrolase-like, type 3
1.03	0	Os01g0759700	HCNGP-like family protein
1.16	0	Os03g0277300	Heat shock protein 70
1.75	0	Os02g0711300	Heat shock protein Hsp20
1.27	0	Os01g0180800	Heat shock protein Hsp70
1.49	0	Os05g0530400	Heat stress transcription factor Spl7
1.13	0	Os02g0530100	Heavy metal transport/detoxification protein
1.12	0	Os10g0532300	Heavy metal transport/detoxification protein
1.3	0	Os01g0196300	Helix-loop-helix DNA-binding
1.28	0	Os02g0116600	Helix-loop-helix DNA-binding
1.28	0	Os05g0529200	Helix-loop-helix DNA-binding
1.37	0	Os05g0139100	Helix-loop-helix DNA-binding
1.15	0	Os12g0106900	Hemopexin domain containing protein
1.38	0	Os05g0305700	Homeodomain-like containing protein
1.47	0	Os06g0670300	Homeodomain-like containing protein
1.09	0	Os07g0136800	Homeodomain-like containing protein
1.29	0	Os02g0220700	Hypothetical conserved gene
1.42	0	Os12g0568166	Immunoglobulin/major histocompatibility complex
1.03	0	Os10g0540900	Inorganic pyrophosphatase
1.14	0	Os02g0169900	Inositol monophosphatase
1.51	0	Os07g0588000	Interferon-related developmental regulator
1.97	0	Os05g0535900	IQ calmodulin-binding region
1.27	0	Os03g0748700	Iron hydrogenase
2.14	0	Os09g0498600	K Homology, type 1, subgroup
1.31	0	Os03g0171600	Kelch-type beta propeller
1.13	0	Os07g0694700	L-ascorbate peroxidase
1.13	0	Os07g0694700	L-ascorbate peroxidase
1.14	0	Os03g0843300	Late embryogenesis abundant protein 2
1	0	Os03g0232800	Lecithin:cholesterol acyltransferase
1.56	0	Os12g0211500	Leucine-rich repeat, N-terminal
1.18	0	Os12g0215950	Leucine-rich repeat, N-terminal
1.35	0	Os07g0176500	Leucine-rich repeat, plant specific containing protein
1.09	0	Os12g0139600	L-Galactono-1,4-lactone dehydrogenase
1.17	0	Os01g0900400	Lipase, class 3
1.62	0	Os03g0636800	LSTK-1-like kinase
1.03	0	Os02g0274900	Major facilitator superfamily
1.34	0	Os10g0558800	Major facilitator superfamily
1.09	0	Os11g0135900	Major facilitator superfamily
1.01	0	Os04g0573000	Major facilitator superfamily MFS_1 protein
1.16	0	Os12g0632700	Malate dehydrogenase, glyoxysomal precursor

1.04	0	Os01g0723400	Malic oxidoreductase
1.33	0	Os01g0138900	Mandelate racemase/muconate lactonizing enzyme
1.1	0	Os02g0676000	Membrane bound O-acyl transferase, MBOAT
2.43	0	Os12g0571000	Metallothionein-like protein type 1
1.11	0	Os03g0606200	Mitochondrial ATP synthase 6 KD subunit
1.14	0	Os01g0225000	Mitochondrial carrier protein
1.08	0	Os01g0571000	Mitochondrial carrier protein
1.19	0	Os01g0143800	Mitochondrial glycoprotein
1.27	0	Os01g0661500	Mov34/MPN/PAD-1
1.23	0	Os08g0180000	mRNA capping enzyme, large subunit family protein
1.07	0	Os01g0684900	Multi antimicrobial extrusion protein MatE
1.16	0	Os10g0345100	Multi antimicrobial extrusion protein MatE
1.54	0	Os12g0125800	Multi antimicrobial extrusion protein MatE
1.2	0	Os07g0484700	Myb transcription factor
1.2	0	Os08g0556700	Myotubularin-related
1.74	0	Os05g0110300	NAD(P)-binding
1.03	0	Os10g0417600	NAD(P)-binding
1.01	0	Os01g0520600	NB-ARC
1.29	0	Os01g0721100	NB-ARC
1.01	0	Os01g0721400	NB-ARC
1.13	0	Os05g0479800	NB-ARC
1.6	0	Os11g0677000	NB-ARC
1.72	0	Os12g0467300	NB-ARC
1.19	0	Os03g0156700	Nickel/cobalt transporter, high-affinity
2.05	0	Os01g0104200	No apical meristem (NAM) protein
1.2	0	Os01g0884300	No apical meristem (NAM) protein
2.48	0	Os02g0594800	No apical meristem (NAM) protein
1.78	0	Os10g0414000	No apical meristem (NAM) protein
1.27	0	Os12g0477400	No apical meristem (NAM) protein
2.72	0	Os10g0386601	Non-protein coding gene
1.64	0	Os01g0591500	Non-protein coding transcript
1.7	0	Os04g0138432	Non-protein coding transcript
2.64	0	Os04g0266200	Non-protein coding transcript
1.56	0	Os02g0568200	NPH3 domain containing protein
1.3	0	Os06g0618000	Nse4 domain containing protein
1.14	0	Os01g0846000	Nucleic acid-binding, OB-fold
1.11	0	Os01g0956600	Nucleotide-binding, alpha-beta plait
1.54	0	Os08g0483200	Nucleotide-binding, alpha-beta plait
1.39	0	Os09g0549500	Nucleotide-binding, alpha-beta plait
1.02	0	Os12g0225100	Nucleotide-binding, alpha-beta plait
1.41	0	Os11g0531700	NUDIX hydrolase
1.45	0	Os01g0238700	Oligopeptide transporter OPT super
1.26	0	Os08g0154000	O-methyltransferase, family 3 protein
1.56	0	Os12g0154700	Oryza sativa germin-like protein 12-1
1.52	0	Os08g0189500	Oryza sativa germin-like protein 8-6
1.69	0	Os08g0189600	Oryza sativa germin-like protein 8-7

1.79	0	Os04g0619500	Ovarian tumour, otubain
1.2	0	Os03g0106300	PAIR1 protein
1.12	0	Os08g0408500	Pathogenesis-related transcriptional factor and ERF
2.5	0	Os09g0572000	Pathogenesis-related transcriptional factor and ERF
1.3	0	Os10g0407000	Pectin lyase fold/virulence factor
1.15	0	Os01g0311700	Pectinesterase inhibitor
1.33	0	Os03g0100100	Pectinesterase inhibitor
1.23	0	Os01g0852900	Pentatricopeptide repeat
1.16	0	Os02g0290000	Pentatricopeptide repeat
1.67	0	Os03g0201400	Pentatricopeptide repeat
1.01	0	Os03g0844000	Pentatricopeptide repeat
1.18	0	Os05g0294600	Pentatricopeptide repeat
2.29	0	Os08g0434000	Pentatricopeptide repeat
1.37	0	Os08g0481000	Pentatricopeptide repeat
1.26	0	Os10g0181200	Pentatricopeptide repeat
1.12	0	Os10g0477200	Pentatricopeptide repeat
1.32	0	Os10g0497300	Pentatricopeptide repeat
1.76	0	Os12g0181900	Pentatricopeptide repeat
1.72	0	Os12g0557800	Pentatricopeptide repeat
1.44	0	Os01g0178600	Peptidase A1
1.25	0	Os09g0482200	Peptidase A1
1.1	0	Os07g0568500	Peptidase aspartic, active site
1.02	0	Os08g0207800	Peptidase aspartic, catalytic
1.05	0	Os02g0654500	Peptidase C12, ubiquitin carboxyl-terminal hydrolase 1
1	0	Os01g0138800	Peptidase C26
1.02	0	Os02g0770700	Peptidase C50, separase
1.1	0	Os09g0362500	Peptidase M1, membrane alanine aminopeptidase
1.68	0	Os02g0740700	Peptidase M10A and M12B, matrixin and adamalysin
1.5	0	Os12g0597500	Peptidase M20
1.09	0	Os12g0563500	Peptidase M24
1.45	0	Os02g0687900	Peptidase S10, serine carboxypeptidase
1.21	0	Os05g0582500	Peptidase S10, serine carboxypeptidase
2.54	0	Os11g0156200	Peptidase S28
1.37	0	Os10g0451900	Peptidase S8 and S53, subtilisin, kexin, sedolisin
1.62	0	Os08g0149000	Peptidase, trypsin-like serine and cysteine
1.15	0	Os02g0168700	Peptidyl-prolyl cis-trans isomerase, FKBP-type
1.38	0	Os02g0751600	Peptidyl-prolyl cis-trans isomerase, FKBP-type
1.27	0	Os03g0302000	Peroxisomal biogenesis factor 11
2.85	0	Os03g0830400	PGPS/D12
1.06	0	Os02g0704500	Phosphatidic acid phosphatase type 2/haloperoxidase
1.01	0	Os03g0805400	Phosphatidic acid phosphatase type 2/haloperoxidase
1.07	0	Os04g0668700	Phosphatidylinositol 3- and 4-kinase, catalytic
1.29	0	Os03g0287100	Phosphatidylinositol transfer protein
1.11	0	Os04g0469500	Phosphofructokinase
1.02	0	Os02g0114400	Phospholipid/glycerol acyltransferase
1.34	0	Os11g0679700	Phospholipid/glycerol acyltransferase

1.58	0	Os12g0563000	Phospholipid/glycerol acyltransferase
1.19	0	Os01g0827200	Phox-like domain containing protein
1.08	0	Os03g0708100	Phytanoyl-CoA dioxygenase
1.16	0	Os06g0729000	Phytoene synthase 1
1.32	0	Os12g0263600	Pinoresinol-lariciresinol reductase TH1
2.37	0	Os10g0491000	Plant Basic Secretory Protein
1.4	0	Os11g0214900	Plant disease resistance response protein
2.01	0	Os12g0567800	Plant metallothionein, family 15 protein
1.01	0	Os01g0763600	PLC-like phosphodiesterase, TIM beta/alpha-barrel
1.98	0	Os02g0187400	PLC-like phosphodiesterase, TIM beta/alpha-barrel
1.52	0	Os03g0230300	Poly (ADP-ribose) polymerase, catalytic region
1.98	0	Os07g0526400	Polyketide synthase, type III
1.05	0	Os02g0161900	Polyubiquitin
1.14	0	Os12g0555500	Probenazole-inducible protein PBZ1
1.53	0	Os02g0694800	Protein kinase
1.09	0	Os06g0660800	Protein kinase
1.12	0	Os01g0747400	Protein kinase, core
1.09	0	Os01g0822200	Protein kinase, core
1.56	0	Os03g0297800	Protein kinase, core
1.16	0	Os05g0560300	Protein kinase, core
1.09	0	Os06g0639500	Protein kinase, core
1.06	0	Os07g0171300	Protein kinase, core
1.27	0	Os09g0110100	Protein kinase, core
1.26	0	Os01g0721800	Protein kinase-like
1.07	0	Os01g0164600	Protein phosphatase 2C-related
1.28	0	Os08g0393600	Protein-tyrosine phosphatase-like, PTPLA
1.34	0	Os03g0152700	Pseudouridine synthase
1.57	0	Os07g0139000	Putative zinc finger CCCH
1.1	0	Os01g0830100	Pyridine nucleotide-disulphide oxidoreductase
2.12	0	Os07g0564500	Pyridine nucleotide-disulphide oxidoreductase
1.08	0	Os03g0848100	Pyridoxal phosphate-dependent transferase
1.09	0	Os01g0178000	Pyridoxal phosphate-dependent transferase
1.31	0	Os01g0736400	Pyridoxal phosphate-dependent transferase
1	0	Os11g0216000	Pyruvate kinase
1.93	0	Os05g0153200	Region of unknown function XH
1.11	0	Os01g0725600	Regulator of chromosome condensation, RCC1
1.03	0	Os12g0284000	Regulator of chromosome condensation, RCC1
1.13	0	Os03g0769600	ResB-like family protein
1.06	0	Os01g0810100	Ribonuclease III
1.93	0	Os02g0652600	Ribosomal protein L19
1.18	0	Os05g0270000	Ribosomal protein L25
1.04	0	Os04g0613600	Ribosomal protein S17
1.36	0	Os03g0687800	Ribosome-inactivating protein
1.58	0	Os10g0570700	Ribosome-inactivating protein
1.55	0	Os10g0569400	RIR1a protein precursor
1.32	0	Os04g0465700	RNA-dependent RNA polymerase, eukaryotic-type

1.22	0	Os02g0707900	Rossmann-like alpha/beta/alpha sandwich fold
1.37	0	Os01g0901900	S1, RNA binding domain containing protein
1.29	0	Os02g0115600	S1, RNA binding domain containing protein
1.26	0	Os01g0876400	Sad1/UNC-like, C-terminal
2.66	0	Os02g0719600	SAM dependent carboxyl methyltransferase
1.05	0	Os11g0112800	Saposin-like domain containing protein
1.33	0	Os02g0202700	Serine acetyltransferase
1.12	0	Os12g0257000	Serine carboxypeptidase I precursor (EC 34165)
1.09	0	Os03g0401100	Serine/threonine protein kinase
1.07	0	Os07g0134600	Serine/threonine protein kinase
1.25	0	Os07g0141200	Serine/threonine protein kinase
1.14	0	Os10g0518800	Serine/threonine protein kinase
1.04	0	Os01g0607900	Serine/threonine protein kinase-related
1.1	0	Os01g0670100	Serine/threonine protein kinase-related
1.13	0	Os01g0927500	Serine/threonine protein kinase-related
1.77	0	Os05g0166600	Serine/threonine protein kinase-related
1.53	0	Os09g0561500	Serine/threonine protein kinase-related
1.61	0	Os10g0468500	Serine/threonine protein kinase-related
1.68	0	Os12g0608500	Serine/threonine protein kinase-related
1.08	0	Os03g0390200	Serine/threonine-protein kinase SAPK1
1	0	Os05g0144400	Serine/threonine-specific protein phosphatase and bis
1.02	0	Os03g0129100	Seven transmembrane protein MLO2
1.05	0	Os06g0225800	Shikimate kinase
1.12	0	Os04g0531900	Short-chain dehydrogenase/reductase SDR
2.05	0	Os07g0664400	Short-chain dehydrogenase/reductase SDR
1.1	0	Os01g0134800	Similar to (1,4)-beta-xylan endohydrolase
1.47	0	Os01g0634300	Similar to 10A19I11
1.04	0	Os02g0771600	Similar to 1-aminocyclopropane-1-carboxylate oxidase
1.9	0	Os07g0638400	Similar to 1-Cys peroxiredoxin
1.26	0	Os03g0243300	Similar to 26S proteasome non-ATPase
1.37	0	Os03g0576400	Similar to 26S proteasome subunit RPN6a
1.23	0	Os12g0183200	Similar to 3' (2'),5'-bisphosphate nucleotidase
1.23	0	Os03g0315800	Similar to 30S ribosomal protein S1
1.83	0	Os06g0263400	Similar to 3-ketoacyl-CoA synthase
1.14	0	Os12g0605800	Similar to 3-methylcrotonyl CoA carboxylase
1.26	0	Os03g0424500	Similar to 40S ribosomal protein S19-2
1.13	0	Os02g0168100	Similar to 4-hydroxyphenylpyruvate dioxygenase
1.03	0	Os05g0519600	Similar to 4-methyl-5(B-hydroxyethyl)-thiazol
1.33	0	Os03g0265400	Similar to 50S ribosomal protein L4
1.13	0	Os08g0558800	Similar to 60S ribosomal protein L10a-3
1.93	0	Os07g0523300	Similar to 60S ribosomal protein L44
1.12	0	Os05g0458400	Similar to AAA-metalloprotease FtsH.
1.15	0	Os09g0472100	Similar to ABC transporter
1.31	0	Os09g0572400	Similar to Abcf2-prov protein
1.06	0	Os02g0766700	Similar to Abscisic acid responsive elements-binding
2.29	0	Os04g0389800	Similar to Acetohydroxyacid synthase

1.68	0	Os01g0110400	Similar to Acetyl-CoA C-acetyltransferase
1.33	0	Os03g0238700	Similar to Acid phosphatase type 5
1.84	0	Os06g0303400	Similar to aconitate hydratase, cytoplasmic
1.1	0	Os05g0438800	Similar to Actin 1
1.21	0	Os03g0243100	Similar to Actin-depolymerizing factor 5
1.25	0	Os01g0681200	Similar to Acyl-CoA synthetase
1.32	0	Os06g0158000	Similar to Acyl-CoA synthetase
1.11	0	Os05g0163700	Similar to Acyl-coenzyme A oxidase 4, peroxisomal
2.09	0	Os12g0592400	Similar to adenine phosphoribosyltransferase 1
1.14	0	Os01g0633100	Similar to ADP-glucose pyrophosphorylase subunit SH2
1.18	0	Os01g0706800	Similar to agglutinin
1.05	0	Os01g0654300	Similar to AGL221Wp
1.3	0	Os07g0282300	Similar to Aldehyde oxidase 1 homolog
1.23	0	Os07g0164900	Similar to Aldehyde oxidase-2
1.67	0	Os10g0155500	Similar to Aldose 1-epimerase-like protein
1.18	0	Os01g0847700	Similar to Aldose reductase
1.35	0	Os12g0503000	Similar to Allantoin permease
1.66	0	Os12g0226900	Similar to Allyl alcohol dehydrogenase
1.35	0	Os11g0255500	Similar to Allyl alcohol dehydrogenase;
1.03	0	Os01g0945100	Similar to amino acid transporter
1.58	0	Os02g0191300	Similar to Amino acid transporter-like protein
1.12	0	Os02g0302200	Similar to aminotransferase
1.37	0	Os06g0712800	Similar to Ankyrin-like protein
1.03	0	Os04g0610400	Similar to AP2 RAP26
1.2	0	Os02g0764100	Similar to AP2 RAP28
1.03	0	Os03g0818800	Similar to APETALA2-like protein
1.07	0	Os03g0291500	Similar to Asparagine synthetase
1.14	0	Os07g0485400	Similar to asparaginyl-tRNA synthetase
1.5	0	Os11g0184600	Similar to Aspartic proteinase Asp1
1.09	0	Os08g0532400	Similar to ATI24-7 protein
1.29	0	Os03g0233200	Similar to ATLP-3
1.96	0	Os01g0843300	Similar to ATP/GTP/Ca++ binding protein
1.2	0	Os02g0526400	Similar to ATP-dependent Clp protease ATP-binding
1.13	0	Os01g0200000	Similar to autophagocytosis protein AUT1-like
1.06	0	Os08g0457400	Similar to Avr9/Cf-9 induced kinase 1
2.45	0	Os11g0592000	Similar to Barwin
1.01	0	Os03g0418000	Similar to Basic endochitinase 2 precursor
1.09	0	Os01g0605100	Similar to BCS1 protein-like protein
1.05	0	Os07g0538000	Similar to Beta-1,3-glucanase precursor
1.08	0	Os08g0244500	Similar to Beta-1,3-glucanase-like protein
1.66	0	Os04g0535600	Similar to Beta-fructofuranosidase 1 precursor
1.21	0	Os07g0485100	Similar to Beta-ureidopropionase
1.24	0	Os06g0184000	Similar to BHLH transcription factor
1.07	0	Os11g0566800	Similar to Bibenzyl synthase
1.84	0	Os11g0555300	Similar to Blast resistance protein Pi37

1.21	0	Os03g0231600	Similar to Branched-chain-amino-acid aminotransferase
1.79	0	Os07g0170000	Similar to Brn1-like protein
1.46	0	Os10g0424500	Similar to BTB/POZ
1.67	0	Os12g0601800	Similar to BZIP transcription factor , expressed
1.27	0	Os01g0559600	Similar to C13 endopeptidase NP1 precursor
1.01	0	Os02g0558100	Similar to C1C-Nt1 protein
1	0	Os01g0623200	Similar to C4-dicarboxylate transporter/malic acid t
1.15	0	Os03g0789000	Similar to Calmodulin-domain protein kinase CDPK
1.8	0	Os01g0939100	Similar to Calmodulin-stimulated calcium-ATPase
1	0	Os03g0807400	Similar to Calreticulin 2 precursor
1.11	0	Os04g0620000	Similar to Canalicular multispecific organic anion
1.13	0	Os05g0310500	Similar to Cathepsin B
2.09	0	Os11g0112200	Similar to Cationic peroxidase 1 precursor
1.23	0	Os12g0132200	Similar to CBL-interacting protein kinase 32
1.1	0	Os09g0416800	Similar to CCR4-NOT transcription complex subunit 7
1.58	0	Os08g0495300	Similar to cDNA clone:J013000K10, full insert
1.47	0	Os01g0721300	Similar to cDNA clone:J013002N02, full insert
1.45	0	Os12g0263800	Similar to cDNA clone:J013045C05, full insert
1.37	0	Os11g0205500	Similar to cDNA clone:J023056F18, full insert
2.34	0	Os10g0572800	Similar to cDNA clone:J023132F01, full insert
1.46	0	Os03g0663201	Similar to cDNA clone:J033060E19, full insert
1.52	0	Os01g0374600	Similar to cDNA, clone: J065097H05, full insert
1.19	0	Os02g0731500	Similar to cDNA, clone: J065098J18, full insert
2.04	0	Os01g0804100	Similar to cDNA, clone: J100035A04, full insert
1.26	0	Os12g0639800	Similar to CDS_VAMP
1.79	0	Os04g0103900	Similar to Chalcone synthase
1.4	0	Os06g0196900	Similar to Chaperonin
2.15	0	Os11g0592200	Similar to Chitin-binding allergen Bra r 2
1.76	0	Os10g0567100	Similar to Chlorophyll b synthase
1.08	0	Os10g0546600	Similar to Chloroplast carotenoid epsilon-ring
1.17	0	Os01g0764400	Similar to Chorismate mutase, chloroplast precursor
1.25	0	Os10g0194200	Similar to Cinnamyl alcohol dehydrogenase
1.16	0	Os04g0556400	Similar to Cis-zeatin O-glucosyltransferase 1
1.84	0	Os12g0111800	Similar to Class III peroxidase 136
1.58	0	Os04g0105800	Similar to Class III peroxidase 52
1.18	0	Os05g0573300	Similar to CTP synthase 1
1.58	0	Os03g0327100	Similar to CUC1
1	0	Os10g0471300	Similar to Cyanate lyase (CYN)
1.06	0	Os02g0255000	Similar to Cyclic nucleotide-gated ion channel 1
1.06	0	Os03g0201100	Similar to Cyclophilin-like protein PPIL3b
1.14	0	Os09g0338400	Similar to Cysteine desulfurase
1.12	0	Os01g0935700	Similar to Cytochrome c1, heme protein
1.59	0	Os07g0635300	Similar to Cytochrome P450
1.89	0	Os07g0635500	Similar to Cytochrome P450
1.72	0	Os10g0514450	Similar to Cytochrome P450
1.15	0	Os12g0135050	Similar to Cytochrome P450

1.5	0	Os03g0570100	Similar to Cytochrome P450 79A1
1.02	0	Os04g0180400	Similar to Cytochrome P450 CYP99A1
1	0	Os06g0129900	Similar to Cytochrome P450 CYPD
1.44	0	Os02g0220100	Similar to cytokinin oxidase1
1.18	0	Os04g0319800	Similar to Cytokinin-O-glucosyltransferase 2
1.89	0	Os08g0169400	Similar to cytokinin-O-glucosyltransferase 2
1.24	0	Os02g0504800	Similar to Delta-9 stearoyl-acyl carrier protein
1.07	0	Os03g0740600	Similar to Deoxyhypusine synthase
1.11	0	Os12g0143800	Similar to Disrupted meiotic cDNA 1 protein
1.11	0	Os12g0130200	Similar to D-mannose binding lectin , expressed
1.25	0	Os09g0116800	Similar to DNA binding protein
1.55	0	Os09g0463900	Similar to DNA binding protein
1.13	0	Os01g0874800	Similar to DNA polymerase I
1.88	0	Os11g0154900	Similar to DNA-binding factor of bZIP class
1.47	0	Os08g0290900	Similar to DNA-directed RNA polymerase III
1.14	0	Os10g0124600	Similar to DnaJ
1.13	0	Os03g0276300	Similar to Dof domain, zinc finger , expressed
1.57	0	Os01g0758200	Similar to Dof2
1.54	0	Os07g0503700	Similar to EIF3e
1.26	0	Os10g0516300	Similar to Electron transfer flavoprotein-ubiquinone
1.44	0	Os05g0529700	Similar to electron transporter/ heat shock protein
1.46	0	Os10g0146901	Similar to electron transporter/ thiol-disulfide exchange
1.16	0	Os06g0571400	Similar to Elongation factor 1 gamma-like protein
2.33	0	Os05g0399100	Similar to Endo-1,3;1,4-beta-D-glucanase precursor
1.17	0	Os05g0399200	Similar to Endo-1,3;1,4-beta-D-glucanase precursor
1.6	0	Os02g0570400	Similar to Ent-kaurene synthase 1A
1.9	0	Os12g0491800	Similar to Ent-kaurene synthase 1A
1.19	0	Os01g0650000	Similar to esterase
1.37	0	Os12g0100700	Similar to Exo70 exocyst complex subunit
1.15	0	Os07g0673200	Similar to F22D1614 protein
1.14	0	Os08g0332800	Similar to F7O1823 protein
1.05	0	Os02g0205500	Similar to Fatty acid elongase 1
1.24	0	Os05g0574600	Similar to Fatty acid elongase 1-like protein
1.51	0	Os03g0600800	Similar to F-box
1.03	0	Os05g0160000	Similar to Ferric leghemoglobin reductase
1.23	0	Os05g0458100	Similar to FK506-binding protein 4
1.22	0	Os03g0122300	Similar to Flavanone 3-hydroxylase-like protein
1.1	0	Os04g0623300	Similar to Flavin-containing monamine oxidase
1.03	0	Os07g0148200	Similar to Flavonol 3-O-glucosyltransferase
1.07	0	Os05g0438600	Similar to Fructose-1,6-bisphosphatase 2
1.09	0	Os05g0402700	Similar to Fructose-bisphosphate aldolase
1.11	0	Os03g0832600	Similar to Galactokinase
1.82	0	Os06g0211600	Similar to Galactoside 2-alpha-L-fucosyltransferase
1.15	0	Os10g0408700	Similar to GAMYB-binding protein
1.88	0	Os12g0155000	Similar to germin-like protein subfamily 1 member 8
1.22	0	Os07g0580900	Similar to GGDP synthase

1.08	0	Os08g0187800	Similar to Glucose-6-phosphate/phosphate-translocator
2.5	0	Os02g0755900	Similar to Glucosyltransferase
1.26	0	Os03g0712800	Similar to Glutamine synthetase root isozyme 2
1.12	0	Os10g0369000	Similar to Glutamyl-tRNA synthetase
1.37	0	Os02g0564000	Similar to Glutathione S-transferase
1.13	0	Os09g0467200	Similar to Glutathione S-transferase GST 23
1.53	0	Os01g0353400	Similar to Glutathione S-transferase GST 8
1.04	0	Os11g0642800	Similar to Glutathione synthetase
1.2	0	Os11g0588300	Similar to Glutathione transferase AtGST 10
1.14	0	Os04g0209200	Similar to Glutathione-conjugate transporter AtMRP4
1.02	0	Os08g0126300	Similar to Glyceraldehyde-3-phosphate dehydrogenase
1.05	0	Os12g0632000	Similar to Glycine-rich RNA-binding protein 1
1.06	0	Os08g0148600	Similar to Glycosyltransferase QUASIMODO1
1.67	0	Os01g0276300	Similar to Group 3 late embryogenesis abundant protein
1.19	0	Os05g0580800	Similar to GTP binding protein
1.09	0	Os09g0327100	Similar to GTP-binding protein
1.05	0	Os03g0246800	Similar to Guanine nucleotide-exchange protein GEP2
1.05	0	Os03g0796800	Similar to guanylate-binding
1.35	0	Os04g0101300	Similar to H0102C093 protein
1.29	0	Os04g0675800	Similar to H0103C0610 protein
1.37	0	Os04g0307900	Similar to H0211A121 protein
1.71	0	Os04g0310800	Similar to H0211A1217 protein
1.02	0	Os04g0286000	Similar to H0211A122 protein
1.39	0	Os07g0542800	Similar to H0306B067 protein
1.07	0	Os04g0438101	Similar to H0315A089 protein
1.13	0	Os01g0165600	Similar to H0323C0817 protein
1.03	0	Os04g0202500	Similar to H0512B0111 protein
1.18	0	Os04g0456300	Similar to H0523F077 protein
1.22	0	Os08g0201700	Similar to H0525G0211 protein
1.81	0	Os10g0439800	Similar to H0813E031 protein
2.06	0	Os04g0204100	Similar to H0825G023 protein
1.27	0	Os04g0206000	Similar to H0825G024 protein
1.53	0	Os10g0404900	Similar to HAHB-5
1.27	0	Os03g0113700	Similar to Heat shock 70 kDa protein, mitochondrial
1.5	0	Os08g0500700	Similar to Heat shock protein 82
1.46	0	Os08g0246950	Similar to Heat-shock protein
1.27	0	Os09g0474300	Similar to Heat-shock protein precursor
1.79	0	Os06g0193400	Similar to Helix-loop-helix protein homolog
1.54	0	Os07g0602050	Similar to Helminthosporium carbonum susceptibility1
1.06	0	Os12g0176800	Similar to Heterochromatin protein
1.01	0	Os01g0133400	Similar to Hexose transporter
1.06	0	Os03g0317000	Similar to High-glucose-regulated protein 8-like
2.49	0	Os05g0237800	Similar to Histidine amino acid transporter
1	0	Os05g0186100	Similar to Histidine-containing phosphotransfer protein
1.56	0	Os02g0215200	Similar to Histone deacetylase
1.82	0	Os02g0457100	Similar to Histone H3

1.62	0	Os06g0160001	Similar to histone H3
1.08	0	Os06g0103300	Similar to Homogentisate 1,2-dioxygenase
1.61	0	Os03g0727200	Similar to HOS13 protein
1.4	0	Os04g0234402	Similar to hydrolase, acting on ester bonds
1.91	0	Os11g0117900	Similar to Hydrolase, alpha/beta fold , expressed
1.02	0	Os01g0269000	Similar to Hydroxymethylglutaryl-CoA lyase
1.39	0	Os03g0626000	Similar to IBR , expressed
1.03	0	Os11g0216900	Similar to IDI2
1.03	0	Os07g0592600	Similar to Indole-3-acetic acid-amido synthetase GH33
3.2	0	Os03g0797500	Similar to Indole-3-glycerol phosphate lyase
3.15	0	Os03g0797400	Similar to Indole-3-glycerol phosphate lyase
1.59	0	Os09g0255400	Similar to Indole-3-glycerol phosphate synthase,
1.22	0	Os03g0780500	Similar to inosine-5-monophosphate dehydrogenase 2
2.19	0	Os03g0251600	Similar to integral membrane single C2 domain protein
1.96	0	Os07g0529000	Similar to Isocitrate lyase
1.89	0	Os05g0311801	Similar to Isopentenyl transferase IPT7
1.2	0	Os10g0461100	Similar to Keratin, type II cytoskeletal 1
1.16	0	Os07g0541500	Similar to KI domain interacting kinase 1
1.05	0	Os06g0554700	Similar to Kinesin heavy chain
1.18	0	Os04g0619000	Similar to L13329 protein
3.54	0	Os01g0842400	Similar to Laccase
2.29	0	Os12g0257600	Similar to Laccase-25
1.23	0	Os01g0199300	Similar to lachrymatory factor synthase
1.06	0	Os05g0458300	Similar to L-ascorbate oxidase
1.2	0	Os03g0285700	Similar to L-ascorbate peroxidase
1.2	0	Os03g0285700	Similar to L-ascorbate peroxidase
1.26	0	Os08g0477100	Similar to Latex allergen
1.07	0	Os04g0615100	Similar to Lecithine cholesterol acyltransferase-like
1.16	0	Os07g0131400	Similar to lectin-like receptor kinase 7
1.21	0	Os07g0130400	Similar to Lectin-like receptor kinase 7;2
1.58	0	Os03g0289800	Similar to Leucoanthocyanidin dioxygenase-like protein
1.06	0	Os06g0237300	Similar to LIM domain protein WLIM-1
1.48	0	Os11g0427800	Similar to Lipid transfer protein LPT III
1.53	0	Os03g0700700	Similar to Lipoxygenase
1.16	0	Os11g0147000	Similar to Long chain acyl-CoA synthetase 6
1.16	0	Os12g0143900	Similar to Long chain acyl-CoA synthetase 6
1.51	0	Os12g0563200	Similar to Lozenge protein
1.94	0	Os01g0114700	Similar to LRK33
1.22	0	Os12g0131900	Similar to lyase
1.05	0	Os08g0523000	Similar to MAB1
1.61	0	Os07g0108900	Similar to MADS-box transcription factor 15
1.06	0	Os03g0638200	Similar to Major facilitator super, expressed
1.64	0	Os07g0271600	Similar to MAK16-like protein RBM13
1.05	0	Os01g0829800	Similar to Malate dehydrogenase precursor
1.14	0	Os08g0434300	Similar to Malate dehydrogenase precursor
1.44	0	Os04g0486950	Similar to Malate synthase

1.71	0	Os11g0622800	Similar to Mannitol dehydrogenase
1.3	0	Os03g0415200	Similar to MAP3K protein kinase-like protein
1.43	0	Os01g0503400	Similar to metal transporter Nramp6
1.1	0	Os08g0424200	Similar to Methylcrotonoyl-CoA carboxylase beta chain
1.07	0	Os01g0739000	Similar to Mitochondrial processing peptidase
1.12	0	Os05g0524300	Similar to Mitochondrial processing peptidase
1.57	0	Os02g0258900	Similar to Molybdopterin biosynthesis CNX2 protein
1.16	0	Os08g0557600	Similar to Monodehydroascorbate reductase
1.21	0	Os06g0498800	Similar to MOTHER of FT and TF1 protein
1.39	0	Os03g0142800	Similar to MRP-like ABC transporter
1.07	0	Os03g0773100	Similar to Myb/SANT domain protein
1.35	0	Os12g0271600	Similar to Myosin heavy chain-like
1.07	0	Os12g0641100	Similar to Na+/H+ antiporter
1.59	0	Os07g0138200	Similar to NAC domain protein, IPR003441
1.29	0	Os07g0684800	Similar to NAM / CUC2-like protein
1.09	0	Os11g0161133	Similar to NB-ARC
1.59	0	Os11g0589800	Similar to NB-ARC
1.36	0	Os06g0287000	Similar to NBS-LRR type R protein, Nbs4-Pi
1.39	0	Os08g0470200	Similar to Nectarin III
1.06	0	Os10g0370700	Similar to Nitrate transporter
1.15	0	Os10g0401900	Similar to No apical meristem protein
1.01	0	Os06g0708700	Similar to Nodulin-like protein
1.02	0	Os05g0366800	Similar to Non-cyanogenic beta-glucosidase
1.23	0	Os04g0304200	Similar to Nonphototropic hypocotyl protein 1
1.73	0	Os10g0490800	Similar to NtPRp27
1.23	0	Os03g0430400	Similar to Nuclear protein 5qNCA
1	0	Os05g0589600	Similar to Nuclear RNA binding protein B
1.5	0	Os03g0838800	Similar to nucleic acid binding protein
1.86	0	Os03g0352300	Similar to Nucleolar protein
1.17	0	Os06g0611700	Similar to Nucleosome assembly protein 1-like protein
1.92	0	Os07g0416900	Similar to Omega-6 fatty acid desaturase
1.36	0	Os03g0643300	Similar to Ornithine-oxo-acid transaminase
1.53	0	Os03g0432100	Similar to Orthophosphate dikinase precursor
1.03	0	Os05g0447900	Similar to OSIGBa0092G145 protein
1.7	0	Os02g0593100	Similar to OSIGBa0106G0712 protein
1.09	0	Os04g0607150	Similar to OSIGBa0113I1310 protein
1.2	0	Os04g0464800	Similar to OSIGBa0130P022 protein
1.96	0	Os04g0658700	Similar to OSIGBa0132E09-OSIGBa0108L248 protein
1.18	0	Os04g0370800	Similar to OSIGBa0134J073 protein
1.52	0	Os10g0413600	Similar to OSIGBa0134P1011 protein
1.48	0	Os03g0330800	Similar to OSIGBa0144C234 protein
1.65	0	Os07g0584750	Similar to OSIGBa0147H174 protein
2.13	0	Os07g0186200	Similar to OSIGBa0148I184 protein
1.1	0	Os04g0534100	Similar to OSIGBa0159I107 protein
1.63	0	Os04g0430900	Similar to OSIGBa0160I144 protein
1.01	0	Os07g0683200	Similar to OsNAC6 protein

1.33	0	Os10g0558400	Similar to Oxidoreductase, 2OG-Fe oxygenase
1.19	0	Os10g0558700	Similar to Oxidoreductase, 2OG-Fe oxygenase ,
1.04	0	Os08g0388900	Similar to para-hydroxybenzoate--polyprenyltransferase
1.68	0	Os02g0705400	Similar to Pathogen induced protein 2-4
1.53	0	Os07g0127700	Similar to Pathogenesis-related protein class 1
1.53	0	Os07g0125000	Similar to Pathogenesis-related protein PR-1 precursor
1.58	0	Os12g0448900	Similar to Pathogen-inducible alpha-dioxygenase
1.07	0	Os03g0405500	Similar to PDI-like protein
1.84	0	Os09g0333500	Similar to PDR-like ABC transporter
1.67	0	Os12g0638200	Similar to Peptide transporter
1.01	0	Os03g0719900	Similar to Peptide transporter 1
1.24	0	Os01g0844300	Similar to Peptidylprolyl isomerase
1.2	0	Os07g0531400	Similar to Peroxidase 27 precursor
1.2	0	Os12g0291100	Similar to Petunia ribulose 1,5-bisphosphate
3.12	0	Os03g0830500	Similar to PGPS/D12
1.14	0	Os04g0518400	Similar to Phenylalanine ammonia-lyase
1.85	0	Os03g0805700	Similar to pheophorbide a oxygenase
1.55	0	Os02g0139000	Similar to Phosphate starvation regulator protein
1.09	0	Os01g0758400	Similar to Phosphatidate cytidylyltransferase
1.11	0	Os05g0545000	Similar to Phosphatidylinositol transfer-like protein IV
1.12	0	Os08g0484500	Similar to Phospho-2-dehydro-3-deoxyheptonate
1.4	0	Os10g0442100	Similar to Phosphoglycerate kinase
1.16	0	Os05g0127200	Similar to Phospholipase C
1.27	0	Os03g0126000	Similar to Phosphorybosyl anthranilate transferase 1
1.1	0	Os06g0502800	Similar to Plant protein , expressed
1.85	0	Os07g0448100	Similar to Plasma membrane integral protein ZmPIP2-6
1.38	0	Os02g0797500	Similar to Plastidic aspartate aminotransferase
1.39	0	Os01g0609300	Similar to Pleiotropic drug resistance protein 3
1.29	0	Os07g0467600	Similar to Plus agglutinin
1.07	0	Os02g0456800	Similar to Pollen signalling protein with adenylyl
2.06	0	Os01g0351200	Similar to Poly
1.06	0	Os04g0628100	Similar to Polyubiquitin
1.06	0	Os07g0509200	Similar to Potassium transporter 7
1.7	0	Os08g0517200	Similar to Potential calcium-transporting ATPase 9
1.02	0	Os11g0141000	Similar to PP2A regulatory subunit-like protein
1.12	0	Os03g0309800	Similar to PPR2
1.05	0	Os11g0107600	Similar to prenylated Rab receptor 2
1.41	0	Os03g0813200	Similar to prohibitin1
1.98	0	Os04g0561500	Similar to Prolyl endopeptidase
1.07	0	Os04g0432500	Similar to Protein disulfide isomerase
1.1	0	Os04g0543000	Similar to Protein kinase
1.23	0	Os12g0149700	Similar to Protein kinase KIPK
1.1	0	Os01g0114100	Similar to Protein kinase RLK17
1.02	0	Os01g0295700	Similar to Protein phosphatase-2C
2.47	0	Os01g0160800	Similar to Protein synthesis inhibitor II
1.43	0	Os01g0150500	Similar to Protein tyrosine phosphatase-like protein

1.2	0	Os03g0734300	Similar to Proteinase inhibitor type II CEVI57
1.19	0	Os09g0511700	Similar to Prunasin hydrolase isoform PH C precursor
2.04	0	Os08g0400000	Similar to Puromycin-sensitive aminopeptidase
1.25	0	Os03g0238600	Similar to Purple acid phosphatase
1.18	0	Os01g0160100	Similar to Pyruvate decarboxylase isozyme 2
1.01	0	Os05g0536900	Similar to RAB7A
1.16	0	Os07g0195100	Similar to Ras-related protein ARA-3
1.13	0	Os03g0191400	Similar to ras-related protein Rab-6A
1.12	0	Os08g0374600	Similar to Receptor kinase-like protein
1.71	0	Os05g0463000	Similar to Receptor protein kinase-like protein
1.42	0	Os07g0574100	Similar to receptor-kinase isolog
1.07	0	Os03g0773700	Similar to Receptor-like protein kinase 2
1.03	0	Os04g0631800	Similar to Receptor-like protein kinase 5
1.18	0	Os10g0389200	Similar to Red chlorophyll catabolite reductase
1.16	0	Os02g0762100	Similar to Regulator of ribonuclease-like protein 2
1.49	0	Os05g0307400	Similar to Regulatory associated protein of mTOR
1.52	0	Os03g0255100	Similar to Relative to SR12 protein
1.52	0	Os11g0252900	Similar to retrotransposon protein
1.02	0	Os09g0482680	Similar to Ribonuclease Z, chloroplast precursor
1.01	0	Os06g0168600	Similar to Ribonucleotide reductase
1.67	0	Os01g0612100	Similar to ribosomal protein S11 containing protein
1.21	0	Os11g0707000	Similar to Ribulose-bisphosphate carboxylase activase
1.5	0	Os05g0145000	Similar to Ring finger protein
1.21	0	Os02g0743700	Similar to RING-H2 finger protein ATL1Q
2.46	0	Os02g0572300	Similar to RING-H2 finger protein ATL3B
1.19	0	Os10g0575200	Similar to Rme-8 homologue
1.18	0	Os05g0427300	Similar to RNA binding protein
1.02	0	Os04g0625800	Similar to RNA Binding Protein 45
1.19	0	Os02g0723600	Similar to RNA polymerase Rpb3/Rpb11 dimerisation
1.22	0	Os04g0679800	Similar to RNA-binding protein-like protein
1.7	0	Os11g0218200	Similar to RNApol24
1.26	0	Os01g0781200	Similar to Rust resistance protein
1.26	0	Os02g0754100	Similar to S1 self-incompatibility locus-linked pollen
1.11	0	Os12g0137200	Similar to Saccharopine dehydrogenase , expressed
1.59	0	Os01g0293000	Similar to S-adenosylmethionine synthetase 1
1.08	0	Os04g0252400	Similar to Sec1p-like protein 1
1.12	0	Os05g0268500	Similar to Serine carboxypeptidase 2
1.06	0	Os03g0333500	Similar to serine/threonine-protein kinase AtPK19
2.07	0	Os05g0433100	Similar to Serine/threonine-protein kinase SAPK7
1.89	0	Os07g0664300	Similar to Short-chain dehydrogenase/reductase
1.14	0	Os05g0263100	Similar to SHR5-receptor-like kinase
1.22	0	Os05g0509500	Similar to Signal recognition particle 54 kDa protein 2
1.5	0	Os06g0473100	Similar to signal recognition particle receptor beta
1.29	0	Os12g0612400	Similar to S-locus protein 5
1.17	0	Os02g0133400	Similar to SMC3 protein
1.68	0	Os03g0829200	Similar to Soluble epoxide hydrolase

1	0	Os05g0438500	Similar to Soluble inorganic pyrophosphatase
1.73	0	Os03g0197200	Similar to Sorbitol transporter
1.15	0	Os11g0637200	Similar to Sorbitol transporter
1.16	0	Os01g0210500	Similar to SOUL-like protein
1.1	0	Os09g0507100	Similar to Squamosa-promoter binding-like protein 11
1.14	0	Os05g0191500	Similar to stem 28 kDa glycoprotein
1.36	0	Os06g0522650	Similar to sterol-8,7-isomerase
1.61	0	Os01g0615100	Similar to Substilin /chymotrypsin-like inhibitor
2.72	0	Os02g0270200	Similar to Subtilase
2.23	0	Os02g0270800	Similar to Subtilase
1.51	0	Os02g0198700	Similar to Subtilisin-like protease
1.28	0	Os11g0637100	Similar to Sugar transporter
1.02	0	Os01g0265800	Similar to Sulfated surface glycoprotein 185 precursor
2.4	0	Os12g0442800	Similar to Sulfite oxidase
1.54	0	Os07g0512200	Similar to Symbiosis-related like protein
1.02	0	Os08g0191600	Similar to Symbiosis-related like protein
1.9	0	Os10g0527800	Similar to Tau class GST protein 3
1.23	0	Os10g0529400	Similar to Tau class GST protein 4
1.26	0	Os06g0687700	Similar to T-complex protein 1, eta subunit
1.28	0	Os02g0247200	Similar to T-complex protein 1, gamma subunit
1.71	0	Os03g0848700	Similar to TDRGA-1
1.15	0	Os06g0181300	Similar to terminal acidic SANT 1
2.41	0	Os07g0218200	Similar to terpene synthase 7
1.22	0	Os03g0663400	Similar to Thaumatin-like protein
1.54	0	Os12g0629700	Similar to Thaumatin-like protein precursor
1.34	0	Os12g0630100	Similar to Thaumatin-like protein precursor
1.49	0	Os02g0538000	Similar to Threonyl-tRNA synthetase
1.14	0	Os09g0388701	Similar to transcription factor jumonji
1.05	0	Os01g0187900	Similar to Transcription factor MYBS2
1.73	0	Os11g0175700	Similar to Transcription factor PCF3
1.87	0	Os02g0168200	Similar to Transfactor-like protein
1.9	0	Os06g0724600	Similar to Transformer-SR ribonucleoprotein
1.19	0	Os07g0571500	Similar to Transmembrane protein 49
1.35	0	Os06g0632300	Similar to Transposon protein
1.59	0	Os01g0253900	Similar to triacylglycerol lipase
1.01	0	Os01g0655300	Similar to Trithorax 4
2.31	0	Os08g0140300	Similar to Tryptophan decarboxylase
1.58	0	Os04g0692100	Similar to Tubulin folding cofactor B
1.82	0	Os09g0439500	Similar to Type II chlorophyll a/b binding protein
1.03	0	Os09g0321900	Similar to Ubiquitin-conjugating enzyme E2 M
1.63	0	Os10g0190000	Similar to Ubiquitin-conjugating enzyme E2 M
1.04	0	Os09g0323000	Similar to UDP-galactose 4-epimerase-like protein
1.19	0	Os11g0446700	Similar to UDP-glucoronosyl and UDP-glucosyl
1.06	0	Os09g0526700	Similar to UDP-glucose 4-epimerase
1	0	Os01g0867600	Similar to UDP-glucose:sterol glucosyltransferase
1.23	0	Os05g0387200	Similar to UDP-sulfoquinovose synthase, chloroplast

1.05	0	Os04g0596400	Similar to UPF0195 protein CG30152
1.15	0	Os12g0502800	Similar to Ureide permease 1
1.41	0	Os01g0965400	Similar to Uridylate kinase
1.19	0	Os03g0835400	Similar to Uvs101
1.49	0	Os01g0962300	Similar to Vacuolar ATP synthase 16 kDa proteolipid
1.58	0	Os01g0659200	Similar to Vacuolar ATP synthase subunit E
1.12	0	Os07g0680000	Similar to Vacuolar sorting receptor 1 precursor
1.17	0	Os01g0232400	Similar to VHS1 protein
1.03	0	Os04g0379700	Similar to Violaxanthin de-epoxidase
3.81	0	Os02g0112900	Similar to Viroid RNA-binding protein
1.26	0	Os04g0614600	Similar to Viroid RNA-binding protein
1.21	0	Os02g0748300	Similar to VMP3 protein
1.06	0	Os12g0116400	Similar to WRKY DNA binding , expressed
2.77	0	Os01g0734000	Similar to WRKY DNA binding protein
1.08	0	Os01g0246700	Similar to WRKY transcription factor 1
1.5	0	Os05g0571200	Similar to WRKY transcription factor 19
1.41	0	Os06g0649000	Similar to WRKY transcription factor 28
1.26	0	Os11g0116900	Similar to WRKY transcription factor 46
1.46	0	Os06g0158100	Similar to WRKY transcription factor 63
1.56	0	Os12g0116700	Similar to WRKY transcription factor 64
1.15	0	Os04g0471700	Similar to WRKY10
2.42	0	Os05g0528500	Similar to WRKY23
1.7	0	Os03g0758950	Similar to WRKY58
1.21	0	Os12g0285400	Similar to Xylanase inhibitor protein 2
1.31	0	Os03g0144800	Similar to Xyloglucan galactosyltransferase
1.4	0	Os01g0201100	Similar to xylosyltransferase oxt
1.43	0	Os05g0588800	Similar to Yarrowia lipolytica chromosome D
1.1	0	Os07g0584000	Similar to Yippee-like protein CG15309
1.06	0	Os01g0679900	Similar to Ythdf2-prov protein
1.05	0	Os01g0593100	Similar to ZCW7
1.35	0	Os11g0243300	Similar to ZF-HD protein dimerisation region
1.03	0	Os05g0397650	Similar to Zinc finger, RING-type
1.53	0	Os07g0232800	Similar to Zinc transporter protein ZIP1
1.5	0	Os03g0284800	Spo11/DNA topoisomerase VI, subunit A
1.01	0	Os03g0170900	Sucrose transporter
1.03	0	Os01g0127300	SufBD family protein.
1.51	0	Os04g0679000	Sugar/inositol transporter
1.34	0	Os11g0594000	Sugar/inositol transporter
1.62	0	Os01g0593700	Sulphate transporter
1.14	0	Os08g0244100	Syntaxin 6, N-terminal
2.58	0	Os03g0362500	Terpenoid synthase
1.46	0	Os04g0345400	Terpenoid synthase
1.29	0	Os01g0358300	Tetratricopeptide-like helical
1.74	0	Os01g0812600	Tetratricopeptide-like helical
1.21	0	Os06g0159600	Tetratricopeptide-like helical
1.13	0	Os01g0103100	TGF-beta receptor, type I/II extracellular region

1.32	0	Os04g0597600	TGF-beta receptor, type I/II extracellular region
1.11	0	Os01g0505400	Thiamine pyrophosphate enzyme, C-terminal TPP-
1.08	0	Os03g0293000	Thioredoxin fold
1.25	0	Os03g0356400	Thioredoxin fold
1.11	0	Os10g0365200	Thioredoxin fold
1.27	0	Os01g0829000	Thioredoxin-like fold
1.18	0	Os04g0395800	Tify domain containing protein
1.01	0	Os01g0775300	TRAF-type
1.07	0	Os01g0817100	TRAM, LAG1 and CLN8 homology
1.24	0	Os05g0485300	TRAM, LAG1 and CLN8 homology
1.33	0	Os09g0372700	TRAM, LAG1 and CLN8 homology
1.35	0	Os11g0166800	Transcription elongation factor, TFIIS/CRSP70, N-t
1.02	0	Os08g0534400	Transcription factor Pcc1
1.14	0	Os09g0534800	Transcription initiation factor IIB
1.34	0	Os07g0550600	Transferase
1.11	0	Os05g0592600	Translation initiation factor 2 related
1.45	0	Os01g0195500	Translation initiation factor SUI1
1.42	0	Os04g0508600	Transmembrane receptor, eukaryota
1.1	0	Os03g0356900	tRNA isopentenyltransferase family protein
1.2	0	Os03g0857400	tRNA-binding arm domain containing protein
1.05	0	Os01g0656600	t-snare domain containing protein
1.23	0	Os01g0644000	Twin-arginine translocation pathway signal
1.28	0	Os03g0724300	Tyrosine protein kinase
1.02	0	Os04g0503600	Tyrosine protein kinase
1	0	Os01g0263600	U5 snRNP-associated 102 kDa protein
1.43	0	Os10g0542200	Ubiquilin
1.13	0	Os03g0405100	Ubiquinone biosynthesis protein COQ9
1.04	0	Os02g0261100	Ubiquitin-conjugating enzyme OsUBC5b
1.15	0	Os01g0176100	UDP-glucuronosyl/UDP-glucosyltransferase
1.08	0	Os01g0620300	UDP-glucuronosyl/UDP-glucosyltransferase
1.01	0	Os01g0736100	UDP-glucuronosyl/UDP-glucosyltransferase
2.11	0	Os05g0527000	UDP-glucuronosyl/UDP-glucosyltransferase
1.99	0	Os05g0527100	UDP-glucuronosyl/UDP-glucosyltransferase
1.39	0	Os05g0527900	UDP-glucuronosyl/UDP-glucosyltransferase
1.32	0	Os09g0482860	UDP-glucuronosyl/UDP-glucosyltransferase
1.48	0	Os09g0518200	UDP-glucuronosyl/UDP-glucosyltransferase
1.22	0	Os10g0548900	diaminopimelate ligase
1.7	0	Os01g0511100	UspA domain containing protein
1.18	0	Os01g0144200	Vacuolar import and degradation protein Vid24
1.2	0	Os03g0679000	Vacuolar import and degradation protein Vid24
1.23	0	Os03g0309000	Virulence factor, pectin lyase fold
1.06	0	Os01g0168500	WD40 repeat-like
1.01	0	Os05g0405900	WD40 repeat-like
1.13	0	Os12g0165000	WD40 repeat-like
1.68	0	Os09g0417800	WRKY transcription factor 62
1	0	Os07g0168800	Zinc finger, AN1-type

1.04	0	Os04g0628400	Zinc finger, BED-type predicted
1.03	0	Os08g0270900	Zinc finger, C2H2-like
1.66	0	Os03g0437200	Zinc finger, C2H2-type
1.22	0	Os06g0727000	Zinc finger, C2H2-type
1.63	0	Os05g0283600	Zinc finger, CCHC-type
1.11	0	Os06g0182500	Zinc finger, LIM-type
1.07	0	Os12g0596800	Zinc finger, LIM-type
1.1	0	Os06g0468400	Zinc finger, PHD-type
1.26	0	Os01g0311400	Zinc finger, RING/FYVE/PHD-type
1.09	0	Os01g0974400	Zinc finger, RING/FYVE/PHD-type
1.2	0	Os02g0539200	Zinc finger, RING/FYVE/PHD-type
1.22	0	Os02g0820200	Zinc finger, RING/FYVE/PHD-type
2.36	0	Os03g0142500	Zinc finger, RING/FYVE/PHD-type
1.06	0	Os03g0188200	Zinc finger, RING/FYVE/PHD-type
1.19	0	Os04g0417400	Zinc finger, RING/FYVE/PHD-type
1.06	0	Os04g0648500	Zinc finger, RING/FYVE/PHD-type
1.14	0	Os06g0318700	Zinc finger, RING/FYVE/PHD-type
1.36	0	Os06g0608800	Zinc finger, RING/FYVE/PHD-type
1.52	0	Os08g0343300	Zinc finger, RING/FYVE/PHD-type
1	0	Os08g0384900	Zinc finger, RING/FYVE/PHD-type
1.24	0	Os10g0142100	Zinc finger, RING/FYVE/PHD-type
1.78	0	Os11g0144500	Zinc finger, RING/FYVE/PHD-type
1.07	0	Os11g0160100	Zinc finger, RING/FYVE/PHD-type
1	0	Os11g0175500	Zinc finger, RING/FYVE/PHD-type
1.45	0	Os11g0542100	Zinc finger, RING-type
1.26	0	Os06g0218200	Zinc finger, SWIM-type
1.11	0	Os12g0181300	Zinc finger, TRAF-type
2.95	0.01	Os03g0661600	Similar to Alpha-amylase/trypsin inhibitor
3.75	0.01	Os10g0504900	Similar to Lipid transfer protein
2.58	0.01	Os02g0749700	Similar to cDNA, clone: J065097H05
2.65	0.01	Os11g0514500	Sorghum bicolor leucine-rich repeat-containing
2.42	0.01	Os07g0418500	Similar to Cytochrome P450
2.78	0.01	Os10g0525600	Similar to Tau class GST protein 3
3.29	0.01	Os05g0399300	Similar to Chitinase
2.44	0.01	Os07g0129200	Similar to Pathogenesis-related protein PR1a
3.32	0.01	Os12g0258700	Cupredoxin
1.8	0.01	Os02g0556000	Similar to cDNA clone:J013112C08, full insert
1.85	0.01	Os12g0268000	Similar to Cytochrome P450 71A1
2.34	0.01	Os09g0368500	Similar to Polyamine oxidase precursor
2.96	0.01	Os03g0790500	Alpha/beta hydrolase fold-3
2.54	0.01	Os08g0112300	Transferase
2.54	0.01	Os11g0684000	Similar to Transcription factor MYB21
2.41	0.01	Os03g0195100	Similar to AGD2
1.59	0.01	Os07g0127500	Similar to PR-1a pathogenesis related protein
2.67	0.01	Os06g0561000	Similar to Myo-inositol oxygenase
2.1	0.01	Os10g0437400	Similar to cDNA, clone: J065097H05

1.5	0.01	Os04g0447700	Similar to Polyketide reductase
1.62	0.01	Os09g0532000	TonB box, conserved site
1.96	0.01	Os11g0700900	Glycoside hydrolase, subgroup, catalytic core
1.98	0.01	Os04g0578000	Similar to 1-aminocyclopropane-1-carboxylate synthase
1.53	0.01	Os08g0485400	Similar to Oxidoreductase
1.96	0.01	Os03g0180800	Tify domain containing protein
1.68	0.01	Os01g0723600	Ribose-phosphate pyrophosphokinase 3
1.42	0.01	Os09g0560700	Molybdenum cofactor sulfurase, C-terminal
1.9	0.01	Os11g0696900	Laccase EC 11032)
2.91	0.01	Os08g0105700	Similar to Cytochrome P450 71C1
1.5	0.01	Os03g0264400	Anthranilate synthase alpha 2 subunit
1.49	0.01	Os12g0431100	ATPase, AAA-type, core
1.52	0.01	Os09g0513100	Lecithin cholesterol acyltransferase-like protein
1.39	0.01	Os05g0120200	Similar to ATPase, coupled to transmembrane
3.39	0.01	Os07g0220200	Similar to H0813E031 protein
1.36	0.01	Os02g0266000	Similar to N-(5'-phosphoribosyl)anthranilate isomerase.
1.5	0.01	Os08g0150700	Cyclin-like F-box domain containing protein
2.55	0.01	Os04g0298700	Clp, N-terminal
1.51	0.01	Os01g0327100	Haem peroxidase
2.31	0.01	Os05g0575000	Similar to predicted protein
2.38	0.01	Os11g0641500	Cupredoxin
1.8	0.01	Os08g0120600	Similar to Fructose-bisphosphate aldolase
2.01	0.01	Os05g0235600	Similar to Nucleosome assembly protein 1-like protein
1.69	0.01	Os09g0454600	Similar to Mitochondrial phosphate transporter
1.62	0.01	Os02g0140400	Similar to Beta-amyrin synthase
2.31	0.01	Os01g0885700	Protein kinase-like
2.58	0.01	Os08g0508000	Cytochrome P450
1.56	0.01	Os07g0245100	Similar to Cytosine deaminase
1.56	0.01	Os02g0102900	Similar to RuBisCO subunit binding-protein beta
2.27	0.01	Os04g0677300	Harpin-induced 1
1.48	0.01	Os05g0516400	Similar to Hydroxyproline-rich glycoprotein DZ-HRGP
1.79	0.01	Os03g0180900	Tify domain containing protein
1.44	0.01	Os11g0105300	Similar to Ammonium Transporter
1.52	0.01	Os09g0551500	Similar to Receptor-like kinase
1.2	0.01	Os12g0583700	Zinc finger, C2H2-type
1.66	0.01	Os01g0128200	Similar to Nuclease I
1.46	0.01	Os06g0486800	Similar to Formate dehydrogenase, mitochondrial
1.81	0.01	Os01g0252700	Phospholipid/glycerol acyltransferase
2.21	0.01	Os02g0650900	Similar to Glutamate dehydrogenase 2
1.51	0.01	Os02g0621300	Fatty acid hydroxylase
1.56	0.01	Os08g0507702	Cytochrome P450
2.13	0.01	Os08g0334900	Xyloglucan fucosyltransferase
1.42	0.01	Os12g0571100	Similar to Metallothionein-like protein type 1
1.86	0.01	Os08g0141400	Similar to External rotenone-insensitive NADPH
1.95	0.01	Os03g0749100	Similar to Beta-glucanase
1.54	0.01	Os07g0182100	Similar to Tryptophan synthase alpha chain

2.02	0.01	Os02g0185400	Cytochrome P450
1.68	0.01	Os12g0541300	Similar to Respiratory burst oxidase homolog protein B
2.1	0.01	Os07g0175600	Plant lipid transfer protein and hydrophobic protein,
2.01	0.01	Os10g0490900	Similar to NtPRp27
1.38	0.01	Os08g0231801	Similar to OSIGBa0125J076 protein
1.79	0.01	Os04g0600300	Alternative oxidase 1b
1.29	0.01	Os08g0176900	Similar to Transcription factor HBP-1b
1.85	0.01	Os11g0592100	Similar to Barwin
1.71	0.01	Os03g0594100	Cytochrome P450
2.25	0.01	Os05g0162000	Similar to Peroxidase
1.38	0.01	Os10g0567300	SH2 motif domain containing protein
1.09	0.01	Os01g0231800	RNA ligase/cyclic nucleotide phosphodiesterase
1.46	0.01	Os01g0876300	F-box associated type 1
1.53	0.01	Os07g0133100	Concanavalin A-like lectin/glucanase, subgroup
1.53	0.01	Os03g0225900	Allene oxide synthase
1.71	0.01	Os07g0125201	Allergen V5/Tpx-1 related
2.1	0.01	Os07g0520800	Ankyrin repeat containing protein
3.36	0.01	Os04g0339000	Cytochrome P450
1.17	0.01	Os04g0513400	Similar to Beta-glucosidase
3.49	0.01	Os06g0127900	Similar to Ribonucleoside-diphosphate reductase
2.78	0.01	Os07g0419100	Cytochrome P450
2.12	0.01	Os12g0564100	Similar to R2R3MYB-domain protein
2.18	0.01	Os04g0583000	Cyclin-like F-box domain containing protein
1.84	0.01	Os03g0571900	Similar to transparent testa 12 protein
1.45	0.01	Os09g0487600	Similar to polygalacturonase
2.38	0.01	Os05g0269100	Cyclin-like F-box domain containing protein
1.55	0.01	Os11g0261900	Metallophosphoesterase
1.99	0.01	Os07g0537400	Similar to Receptor-like protein kinase
1.17	0.01	Os04g0690800	22 kDa protein of photosystem II
1.14	0.01	Os04g0182200	2OG-(FeII) oxygenase
1.26	0.01	Os01g0952800	Achaete-scute transcription factor related
1.08	0.01	Os07g0688800	Aldehyde dehydrogenase
1.06	0.01	Os12g0100500	Alpha/beta hydrolase
1.01	0.01	Os09g0460500	Alpha/beta hydrolase fold-3
1.69	0.01	Os12g0580400	Amino acid/polyamine transporter I
1	0.01	Os02g0601700	Ankyrin repeat containing protein
1.58	0.01	Os03g0362200	Armadillo-like helical
1.07	0.01	Os09g0554300	Auxin efflux carrier
1.02	0.01	Os02g0643800	Auxin responsive SAUR protein
1.63	0.01	Os01g0588400	Band 7 protein family protein
1.54	0.01	Os04g0599300	Basic helix-loop-helix dimerisation region bHLH
1.03	0.01	Os02g0131400	Beta-D-glucan exohydrolase
1.96	0.01	Os09g0423400	Biopterin transport-related protein BT1
1.94	0.01	Os06g0254600	Caleosin related
1.06	0.01	Os01g0314100	Catalytic domain of components of various dehydrogenase

1.14	0.01	Os01g0948300	Cellular retinaldehyde-binding/triple function, C-
1.09	0.01	Os09g0258000	Cellular retinaldehyde-binding/triple function, C-
1.14	0.01	Os02g0778500	Chalcone isomerase
1.03	0.01	Os09g0334800	Concanavalin A-like lectin/glucanase
1.55	0.01	Os06g0338200	Copper amine oxidase
1.18	0.01	Os06g0142100	Cyclin-like F-box domain containing protein
1.27	0.01	Os07g0499900	Cyclin-like F-box domain containing protein
1	0.01	Os12g0267200	Cyclopropane-fatty-acyl-phospholipid synthase
1.42	0.01	Os10g0517500	Cys/Met metabolism, pyridoxal phosphate-dependent
1.08	0.01	Os09g0556500	Cysteinyl-tRNA synthetase, class Ia
1.18	0.01	Os05g0565100	Cytochrome b561/ferric reductase transmembrane
1.19	0.01	Os02g0569000	Cytochrome P450
1.92	0.01	Os02g0569400	Cytochrome P450
1.03	0.01	Os02g0636300	DEAD-like helicase, N-terminal
1	0.01	Os03g0219700	DEAD-like helicase, N-terminal
1.06	0.01	Os01g0626400	DNA-binding protein WRKY2-like
1.03	0.01	Os02g0608400	EF-Hand type
1.09	0.01	Os02g0303500	Eggshell protein
1.25	0.01	Os04g0578600	Ferric reductase-like transmembrane component
1.09	0.01	Os11g0127800	Forkhead-associated
1	0.01	Os01g0692100	Glutathione S-transferase, C-terminal-like
1.39	0.01	Os03g0188500	Glutelin family protein
1.76	0.01	Os05g0247500	Glycoside hydrolase, family 18 protein
1.03	0.01	Os12g0578500	Glycosyl transferase, family 8 protein
1.18	0.01	Os05g0430400	GTP1/OBG domain containing protein
1.02	0.01	Os10g0567900	HAT dimerisation
1	0.01	Os04g0667600	Heavy metal transport/detoxification protein
1.64	0.01	Os10g0506100	Heavy metal transport/detoxification protein
1.41	0.01	Os02g0433600	Helix-loop-helix DNA-binding
1.27	0.01	Os04g0660100	Helix-loop-helix DNA-binding
1.01	0.01	Os08g0490000	Helix-loop-helix DNA-binding
1.39	0.01	Os03g0251350	Histone-fold domain containing protein
1.05	0.01	Os09g0470500	Homeodomain leucine zipper protein
1.06	0.01	Os02g0539600	Homeodomain-like containing protein
1.35	0.01	Os06g0176700	Isopenicillin N synthase
1.19	0.01	Os09g0570800	Isopenicillin N synthase
1.2	0.01	Os02g0101800	Kinesin, motor region
1.68	0.01	Os01g0571800	Lateral organ boundaries, LOB
1.58	0.01	Os01g0881900	Leucine-rich repeat, cysteine-containing containing
1.15	0.01	Os10g0527900	Leucine-rich repeat, N-terminal
1.02	0.01	Os01g0249300	Lg106-like family protein
1.35	0.01	Os01g0936200	Lipase, class 3
1.39	0.01	Os11g0655800	Lipase, class 3
1.06	0.01	Os06g0229400	Lipase, GDSL
1.31	0.01	Os10g0109900	Major facilitator superfamily, general substrate
1.09	0.01	Os09g0544900	MaoC-like dehydratase

1.12	0.01	Os08g0485600	Methyl-CpG DNA binding
2.12	0.01	Os07g0667400	Methyltransferase type 12
1.22	0.01	Os11g0206600	Mitochodrial transcription termination factor-related
1.24	0.01	Os01g0265200	Mitochondrial carrier protein
1.5	0.01	Os12g0123700	NAC- 18
1.05	0.01	Os01g0954000	NADPH-dependent FMN reductase
1.01	0.01	Os11g0588600	NB-ARC
1.23	0.01	Os12g0552900	NB-ARC
1.63	0.01	Os08g0255225	Non-protein coding gene
1.02	0.01	Os03g0736000	NOT2/NOT3/NOT5
1.02	0.01	Os01g0589000	Nucleic acid-binding, OB-fold
1.14	0.01	Os01g0711800	Nucleosome assembly protein (NAP)
1.03	0.01	Os03g0801800	Nucleotide-binding, alpha-beta plait
1.72	0.01	Os07g0631900	Nucleotide-binding, alpha-beta plait
1.05	0.01	Os03g0656900	NusB/RsmB/TIM44
1.11	0.01	Os09g0477900	NusB/RsmB/TIM44
1.03	0.01	Os05g0349700	Oryza sativa yellow-green leaf1
1.03	0.01	Os03g0859800	Ovarian tumour, otubain
1.38	0.01	Os04g0546800	Pathogenesis-related transcriptional factor and ERF
1.22	0.01	Os01g0892600	Pectinacetylesterase
1.21	0.01	Os02g0730900	Pentatricopeptide repeat
1.44	0.01	Os07g0239600	Pentatricopeptide repeat
1.41	0.01	Os08g0191900	Pentatricopeptide repeat
1.43	0.01	Os10g0501200	Pentatricopeptide repeat
1.24	0.01	Os01g0616800	Pentatricopeptide repeat containing protein
1.12	0.01	Os10g0511400	Peptidase S28
1.03	0.01	Os01g0132800	Peptidyl-tRNA hydrolase
1.06	0.01	Os01g0832000	Phosphatidate cytidylyltransferase
1.02	0.01	Os03g0852800	Phosphoesterase
1.09	0.01	Os01g0361500	Phospholipid/glycerol acyltransferase
1.37	0.01	Os04g0613900	Potassium uptake protein, kup
1.15	0.01	Os05g0150000	Proline synthetase co-transcribed bacterial homolog
1.33	0.01	Os01g0690800	Protein kinase, core
1.13	0.01	Os02g0194400	Protein kinase, core
1.18	0.01	Os12g0112500	Protein-tyrosine phosphatase, dual specificity
1	0.01	Os05g0465100	RabGAP/TBC
1.49	0.01	Os01g0178100	Region of unknown function DUF1767
1.5	0.01	Os12g0613600	Remorin, C-terminal region
1.23	0.01	Os02g0102400	Ribosomal protein S5
2.51	0.01	Os03g0327600	Ricin B-related lectin
1.19	0.01	Os09g0552600	RmlC-like jelly roll fold
1.57	0.01	Os12g0154800	RmlC-like jelly roll fold
1.02	0.01	Os01g0558300	RWD domain containing protein
1.04	0.01	Os01g0138400	Serine/threonine protein kinase
1.02	0.01	Os01g0292200	Serine/threonine protein kinase
1.11	0.01	Os04g0202300	Serine/threonine protein kinase-related

1.17	0.01	Os04g0616600	Serine/threonine protein kinase-related
1.47	0.01	Os02g0611300	SET domain containing protein
1.36	0.01	Os06g0299300	Short-chain dehydrogenase/reductase SDR
1.14	0.01	Os07g0190000	Similar to 1-deoxy-D-xylulose 5-phosphate synthase 2
1.76	0.01	Os02g0803700	Similar to 26S protease regulatory subunit 6A homolog
1.01	0.01	Os02g0817700	Similar to 3-ketoacyl-CoA thiolase
1.28	0.01	Os12g0133050	Similar to 60S acidic ribosomal protein P0
1.03	0.01	Os09g0449600	Similar to Aconitate hydratase, cytoplasmic
1.03	0.01	Os03g0845500	Similar to Acyl-CoA synthetase-like protein
1.06	0.01	Os05g0580000	Similar to ADP-glucose pyrophosphorylase
1.2	0.01	Os03g0352500	Similar to AGR379Wp
1.58	0.01	Os07g0281800	Similar to Aldehyde oxidase-2
1.05	0.01	Os09g0567366	Similar to Aldo-keto reductase/ oxidoreductase
1.31	0.01	Os07g0679300	Similar to Alpha-galactosidase precursor
1.53	0.01	Os11g0195600	Similar to Amino acid carrier
1.08	0.01	Os05g0194500	Similar to ANAC075
1.17	0.01	Os01g0735400	Similar to Anthocyanidin 5,3-O-glucosyltransferase
1.17	0.01	Os04g0630900	Similar to Anthocyanidin reductase
1.38	0.01	Os01g0608300	Similar to aspartic proteinase nepenthesin-2
1.07	0.01	Os08g0478200	Similar to ATP synthase D chain, mitochondrial
1.49	0.01	Os07g0192800	Similar to ATPase 3
1.44	0.01	Os12g0472300	Similar to ATPase, AAA
1.21	0.01	Os01g0681400	Similar to Autophagy protein beclin1
1.25	0.01	Os10g0147400	Similar to Auxin influx carrier protein
1.32	0.01	Os06g0242000	Similar to benzoate carboxyl methyltransferase
1.2	0.01	Os07g0240200	Similar to Beta-1,3 glucanase precursor
1.48	0.01	Os01g0940800	Similar to Beta-1,3-glucanase precursor
1.14	0.01	Os05g0199800	Similar to BHLH transcription activator Ivory seed
1.16	0.01	Os07g0170100	Similar to Branched chain alpha-keto acid
1.71	0.01	Os05g0506900	Similar to Brix domain-containing protein 1
1.27	0.01	Os12g0613250	Similar to BTB/POZ; Superoxide dismutase
1.35	0.01	Os07g0124300	Similar to bZIP transcription factor
1.48	0.01	Os03g0322700	Similar to BZIP transcription factor , expressed
1.45	0.01	Os11g0136400	Similar to Carbohydrate transporter/ sugar porter/
1.09	0.01	Os03g0724700	Similar to cDNA clone:002-104-C06, full insert
1.04	0.01	Os09g0452300	Similar to cDNA, clone: J065054A13, full insert
1.23	0.01	Os12g0129650	Similar to cDNA, clone: J065154E06, full insert
1.08	0.01	Os08g0114200	Similar to CEL5
1.16	0.01	Os01g0220100	Similar to Cellulase
1.32	0.01	Os07g0525900	Similar to Chalcone synthase
1.03	0.01	Os03g0300600	Similar to Chaperone protein dnaJ
1.01	0.01	Os03g0835700	Similar to Chloroplast heat shock protein HSP262
1.66	0.01	Os08g0368000	Similar to Coatomer delta subunit
1.66	0.01	Os08g0556900	Similar to Cysteine proteinase
1.28	0.01	Os10g0514700	Similar to Cytochrome P450
1.34	0.01	Os01g0951700	Similar to Cytochrome P450 CYP94E4

1.01	0.01	Os06g0655100	Similar to D-3-phosphoglycerate dehydrogenase
1.14	0.01	Os05g0147500	Similar to DEGP2
1.34	0.01	Os01g0968800	Similar to Dehydration responsive element binding
1.3	0.01	Os06g0499900	Similar to Dihydrolipoamide acetyltransferase (E2)
1.16	0.01	Os12g0497300	Similar to DNA repair protein RAD51 homolog
1.03	0.01	Os02g0799000	Similar to DNA-binding protein phosphatase 2C
1.6	0.01	Os11g0578250	Similar to DnaJ , expressed
1.05	0.01	Os03g0776900	Similar to DNAJ protein-like
1.04	0.01	Os05g0562300	Similar to DnaJ-like protein
1.85	0.01	Os05g0402900	Similar to EDGP
1.54	0.01	Os01g0742200	Similar to Elongation factor EF-2
1.01	0.01	Os12g0541500	Similar to Elongation factor Ts
1.46	0.01	Os02g0654100	Similar to Enoyl-CoA hydratase
1.94	0.01	Os03g0860100	Similar to Ethylene-responsive transcription factor 2
1.96	0.01	Os01g0107600	Similar to Exonuclease
1.08	0.01	Os01g0221700	Similar to F22C129
1.05	0.01	Os06g0684000	Similar to FAD-dependent pyridine
1.2	0.01	Os03g0685000	Similar to Ferredoxin
1.58	0.01	Os06g0486900	Similar to Formate dehydrogenase,
1	0.01	Os06g0652400	Similar to GDP-4-keto-6-deoxy-D-mannose-3, 5..
1.01	0.01	Os03g0313600	Similar to Genes for GrpE, DnaK and DnaJ
1.32	0.01	Os01g0946500	Similar to Glucan endo-1,3-beta-glucosidase GV
1.25	0.01	Os04g0543900	Similar to glutamic dehydrogenase1
1.11	0.01	Os10g0502400	Similar to Glutamyl-tRNA reductase 2
1.02	0.01	Os10g0415300	Similar to Glutathione reductase
1.22	0.01	Os01g0949750	Similar to Glutathione S-transferase GST 28
1.32	0.01	Os10g0530900	Similar to Glutathione S-transferase GST 30
1.01	0.01	Os10g0525800	Similar to Glutathione S-transferase GSTU31
1.08	0.01	Os10g0527100	Similar to Glutathione S-transferase, N-terminal
1.85	0.01	Os10g0530800	Similar to Glutathione transferase
1.3	0.01	Os10g0413400	Similar to Glycerol-3-phosphate acyltransferase 6
1.2	0.01	Os07g0602800	Similar to glycerophosphoryl diester phosphodiesterase
1.23	0.01	Os06g0675600	Similar to GRAB2 protein
1.17	0.01	Os07g0412100	Similar to Granule-bound starch synthase Ib
1.43	0.01	Os01g0902900	Similar to GRAS family transcription factor
2.72	0.01	Os02g0776900	Similar to Growth-regulating factor 1
1.52	0.01	Os07g0636000	Similar to H/ACA ribonucleoprotein complex subunit 4
1.67	0.01	Os04g0623500	Similar to H0215F087 protein
1.05	0.01	Os07g0111301	Similar to H0515C1112 protein
1.91	0.01	Os09g0548700	Similar to H0515C113 protein
1.33	0.01	Os02g0547300	Similar to H0523F077 protein
1.15	0.01	Os09g0491772	Similar to Heat shock protein 70
1.08	0.01	Os08g0546800	Similar to Heat stress transcription factor B-2b
1.55	0.01	Os07g0255200	Similar to Helicase-like protein [Oryza sativa
1.17	0.01	Os02g0214900	Similar to Histone deacetylase HDAC2
1.34	0.01	Os01g0152700	Similar to Histone H2B

1.48	0.01	Os12g0415400	Similar to Histone H3
1.01	0.01	Os04g0583600	Similar to histone H4
1.19	0.01	Os06g0698200	Similar to Homeobox-leucine zipper protein HOX18
1.02	0.01	Os05g0428600	Similar to HSP70 precursor
1.08	0.01	Os08g0398400	Similar to Hypersensitive-induced response protein
1.21	0.01	Os03g0616700	Similar to Importin-beta N-terminal , expressed
1.74	0.01	Os05g0156900	Similar to Inorganic pyrophosphatase
1.02	0.01	Os07g0172900	Similar to Integral membrane protein
1.01	0.01	Os02g0280700	Similar to Iron/ascorbate-dependent oxidoreductase
1.16	0.01	Os09g0507300	Similar to L-ascorbate oxidase precursor
1.11	0.01	Os07g0131500	Similar to lectin-like receptor kinase 7
1.13	0.01	Os07g0283125	Similar to lectin-like receptor kinase 7
1.73	0.01	Os10g0442000	Similar to Lectin-like receptor kinase 7;2
1.08	0.01	Os04g0583900	Similar to LHY protein
1.94	0.01	Os05g0346800	Similar to LOB domain protein 3
1.6	0.01	Os01g0761300	Similar to Long-chain-fatty-acid-CoA ligase-like
1.01	0.01	Os01g0246400	Similar to Low molecular mass early light-inducible
1.2	0.01	Os01g0115600	Similar to LRK14
1.08	0.01	Os03g0710500	Similar to Luminal binding protein
1.93	0.01	Os05g0367800	Similar to Luminal binding protein 2 precursor
1.09	0.01	Os07g0622200	Similar to M-160-u1_1
2.09	0.01	Os12g0107500	Similar to Macrophage migration inhibitory factor
1.48	0.01	Os01g0393400	Similar to MDR-like ABC transporter
1.06	0.01	Os03g0815200	Similar to Methylenetetrahydrofolate reductase
1.69	0.01	Os02g0574000	Similar to Monosaccharide transporter 1
1.3	0.01	Os04g0452600	Similar to Monosaccharide transporter 1
1.6	0.01	Os01g0816100	Similar to NAC domain protein
1.61	0.01	Os10g0494200	Similar to N-acetyl-gamma-glutamyl-phosphate
2.54	0.01	Os07g0602000	Similar to NADPH HC toxin reductase
1.47	0.01	Os01g0698900	Similar to nascent polypeptide-associated complex
1.34	0.01	Os02g0306401	Similar to Nicotianamine aminotransferase A
1.24	0.01	Os04g0538400	Similar to Nodulin 21
1.18	0.01	Os01g0207900	Similar to nodulin-like protein
1.31	0.01	Os03g0323350	Similar to non-cyanogenic beta-glucosidase
1.01	0.01	Os12g0123600	Similar to Nucleoside-triphosphatase
1.06	0.01	Os02g0785900	Similar to nucleotide binding
1.44	0.01	Os11g0303300	Similar to O-methyltransferase
1.32	0.01	Os04g0650000	Similar to Oryzain alpha chain precursor
3.03	0.01	Os04g0344100	Similar to OSIGBa0106G083 protein
1.06	0.01	Os10g0102900	Similar to OSIGBa0140C024 protein
1.05	0.01	Os04g0655700	Similar to OSIGBa0147J1914 protein
1.79	0.01	Os08g0189200	Similar to Oxalate oxidase
1.92	0.01	Os08g0189300	Similar to Oxalate oxidase
1.27	0.01	Os08g0189850	Similar to Oxalate oxidase-like protein or germin-like
1.5	0.01	Os12g0551600	Similar to Patatin-like phospholipase
2.07	0.01	Os11g0614400	Similar to Patatin-like protein 1

1.19	0.01	Os07g0129400	Similar to Pathogenesis-related protein 1
1.15	0.01	Os07g0522500	Similar to PDR6 ABC transporter
1.1	0.01	Os08g0564000	Similar to Phosphate transporter 6
1.03	0.01	Os05g0180600	Similar to Phosphatidylinositol 3-kinase, root isoform
1.23	0.01	Os02g0823100	Similar to Plasma membrane intrinsic protein
1.32	0.01	Os01g0609200	Similar to Pleiotropic drug resistance protein 3
1	0.01	Os08g0254500	Similar to Preprotein translocase secY subunit
1.04	0.01	Os09g0562700	Similar to Pre-pro-TPE4A protein precursor
1.01	0.01	Os03g0339100	Similar to PRL1 protein
1.07	0.01	Os02g0110600	Similar to protein kinase
1.3	0.01	Os12g0145200	Similar to Protein MONOCULM 1
1.29	0.01	Os10g0389300	Similar to Red chlorophyll catabolite reductase
1.31	0.01	Os03g0165400	Similar to Relative to SR12 protein
1.59	0.01	Os01g0106200	Similar to RER1A protein
1.51	0.01	Os11g0133300	Similar to Resistance protein candidate
2.26	0.01	Os06g0257450	Similar to Ribonucleoside-diphosphate reductase
1.02	0.01	Os04g0658300	Similar to Ribulose bisphosphate carboxylase/oxygenase
1.02	0.01	Os01g0618400	Similar to RNA helicase
1.08	0.01	Os07g0633200	Similar to SC35-like splicing factor SCL30a, 30a kD
1.31	0.01	Os03g0738400	Similar to Serine hydroxymethyltransferase, cytosolic
1.12	0.01	Os01g0928700	Similar to Serine palmitoyltransferase
1.08	0.01	Os05g0444500	Similar to solute carrier family 35, member F1
1.42	0.01	Os01g0126900	Similar to spore coat protein-like protein [Oryza sativa
1.02	0.01	Os07g0460100	Similar to stem 28 kDa glycoprotein
1.15	0.01	Os04g0405300	Similar to Stem secoisolariciresinol dehydrogenase
1.05	0.01	Os03g0340500	Similar to Sucrose synthase
1.01	0.01	Os11g0637400	Similar to Sugar transporter , expressed
1.69	0.01	Os07g0665300	Similar to Superoxide dismutase
1.34	0.01	Os07g0519100	Similar to taxane 10-beta-hydroxylase
1.65	0.01	Os12g0629300	Similar to Thaumatin-like protein
1.11	0.01	Os01g0504500	Similar to Transparent testa 12 protein
1.03	0.01	Os11g0549900	Similar to tubulin alpha-6 chain
1.04	0.01	Os11g0644800	Similar to Tyrosine/nicotianamine aminotransferases
1.42	0.01	Os03g0613100	Similar to Ubiquitin-activating enzyme E1 2
1.13	0.01	Os01g0951400	Similar to Uridine 5'-monophosphate synthase
1.31	0.01	Os06g0706600	Similar to wall-associated kinase 3
1.26	0.01	Os09g0561400	Similar to Wall-associated kinase-like 1
1.02	0.01	Os02g0181300	Similar to WRKY transcription factor
1.15	0.01	Os03g0321800	Similar to WRKY transcription factor 55
1.48	0.01	Os07g0529700	Similar to Xyloglucan endotransglucosylase/hydrolase
1.04	0.01	Os03g0820300	Similar to ZPT2-14
1.63	0.01	Os05g0513800	Small GTP-binding protein OsRac2
1.19	0.01	Os03g0343300	Small-subunit processome, Utp14
2.26	0.01	Os01g0235300	SOUL haem-binding protein
1.64	0.01	Os02g0177300	Squamosa-promoter binding protein 1

1.6	0.01	Os04g0179700	Syn-pimara-7,15-diene synthase
2.75	0.01	Os08g0168000	Terpenoid synthase
1.16	0.01	Os02g0580900	TGF-beta receptor, type I/II extracellular region
1.16	0.01	Os05g0198200	Thioredoxin fold
1.08	0.01	Os11g0137500	Transcription factor TFE/TFIIEalpha, HTH domain
1.14	0.01	Os06g0145600	Transferase
1.25	0.01	Os01g0104900	Transferase
1.03	0.01	Os02g0484200	Transferase
1	0.01	Os04g0609500	Transferase
1.05	0.01	Os05g0141300	Transferase
1.14	0.01	Os08g0111800	Transferase
1.05	0.01	Os07g0614600	Transmembrane receptor, eukaryota
1.23	0.01	Os01g0548600	Tyrosine protein kinase
1.01	0.01	Os10g0351500	Tyrosine protein kinase
2.09	0.01	Os03g0425600	UDP-glucose dehydrogenase
1.2	0.01	Os04g0206600	UDP-glucuronosyl/UDP-glucosyltransferase
1.39	0.01	Os04g0523200	Up-frameshift suppressor 2
1.44	0.01	Os01g0201600	Virulence factor, pectin lyase fold
1.76	0.01	Os06g0578700	von Willebrand factor, type A
1.02	0.01	Os11g0610700	WD40 repeat-like
1.81	0.01	Os01g0838600	Zinc finger, C2H2-like
1.11	0.01	Os10g0555300	Zinc finger, C2H2-like
1.02	0.01	Os03g0717600	Zinc finger, C2H2-type matrin
1.15	0.01	Os03g0626600	Zinc finger, LIM-type
1.07	0.01	Os01g0960500	Zinc finger, RING/FYVE/PHD-type
1.15	0.01	Os03g0650900	Zinc finger, RING/FYVE/PHD-type
1.02	0.01	Os04g0418500	Zinc finger, RING/FYVE/PHD-type
1.34	0.01	Os06g0128700	Zinc finger, RING-type
1.87	0.01	Os08g0467400	Zinc/iron permease
1.05	0.02	Os09g0250700	ABC-1
1.31	0.02	Os02g0772300	Acyl-CoA N-acyltransferase
1.07	0.02	Os05g0411200	Adrenodoxin reductase
1.24	0.02	Os04g0635700	Aldehyde dehydrogenase, conserved site
1.19	0.02	Os07g0124900	Allergen V5/Tpx-1 related
1.01	0.02	Os03g0178500	Alpha/beta hydrolase
2.42	0.02	Os03g0203200	Alpha/beta hydrolase fold-1
1.2	0.02	Os06g0228800	Amino acid transporter, transmembrane
1.1	0.02	Os10g0437100	Amino acid/polyamine transporter I
1.82	0.02	Os11g0199000	Ankyrin repeat containing protein
1.13	0.02	Os12g0277400	Armadillo-like helical
1.37	0.02	Os12g0488900	Armadillo-like helical
1.14	0.02	Os03g0153900	Aromatic-ring hydroxylase
1.24	0.02	Os07g0192600	ATPase, AAA-type, core
1.71	0.02	Os03g0804200	Bifunctional inhibitor/plant lipid transfer protein/seed
1.02	0.02	Os08g0375700	BTB/POZ fold domain containing protein
1.26	0.02	Os11g0202200	Cyclin-like F-box domain containing protein

1.09	0.02	Os03g0708600	DEAD-like helicase, N-terminal
1.97	0.02	Os02g0761900	Dimethylmenaquinone methyltransferase
1.21	0.02	Os05g0369500	Exo70 exocyst complex subunit
1.29	0.02	Os05g0247100	Glycoside hydrolase, family 18 protein
1.61	0.02	Os01g0296700	Glycoside hydrolase, family 3, N-terminal
1.02	0.02	Os05g0539400	Glycoside hydrolase, family 35 protein
1.01	0.02	Os10g0140200	Glycoside hydrolase, family 38
1.47	0.02	Os08g0253800	Glycosyl transferase, family 2
1.14	0.02	Os03g0244000	Heat shock protein DnaJ, cysteine-rich region
1.26	0.02	Os05g0163900	Helix-loop-helix DNA-binding
1.13	0.02	Os10g0162600	Lateral organ boundaries, LOB
1.38	0.02	Os12g0562100	Major facilitator superfamily, general substrate
1.08	0.02	Os08g0515800	Mitochodrial transcription termination factor-related
1.4	0.02	Os10g0576900	NAD(P)-binding
1.52	0.02	Os05g0261001	Non-protein coding gene
1.04	0.02	Os07g0249900	Peptidase M20
1.05	0.02	Os06g0318600	Peptidase S41
1.43	0.02	Os02g0615300	Protein kinase, core
2.29	0.02	Os04g0614500	Pyridoxal phosphate-dependent transferase
1.16	0.02	Os10g0512500	RNA-binding, CRM domain
1.53	0.02	Os03g0826700	SAM (and some other nucleotide) binding motif
1.1	0.02	Os09g0356200	Serine/threonine protein kinase
1.42	0.02	Os09g0471550	Serine/threonine protein kinase
1.12	0.02	Os04g0275100	Serine/threonine protein kinase-related
1.3	0.02	Os02g0137200	Similar to 50S ribosomal protein L3-1
2	0.02	Os02g0107900	Similar to ABC transporter family
1.14	0.02	Os07g0108300	Similar to Alanine aminotransferase
1.06	0.02	Os06g0245800	Similar to Alanyl-tRNA synthetase
1.51	0.02	Os01g0168900	Similar to anthocyanin regulatory C1 protein
1.07	0.02	Os06g0679500	Similar to Avr9 elicitor response-like protein
1.23	0.02	Os07g0656200	Similar to Beta-glucosidase
1.12	0.02	Os10g0416200	Similar to Beta-ketoacyl-CoA synthase
1.25	0.02	Os08g0498400	Similar to Caffeoyl-CoA 3-O-methyltransferase
1.15	0.02	Os01g0267900	Similar to Calmodulin NtCaM3
1.13	0.02	Os12g0133300	Similar to Carbohydrate transporter/ sugar porter
1.12	0.02	Os02g0194100	Similar to Citrate synthase
1.02	0.02	Os12g0278700	Similar to cystinosin
1.21	0.02	Os02g0173100	Similar to cytochrome P450
1.37	0.02	Os01g0627600	Similar to Cytochrome P450 CYP72A5
1.12	0.02	Os01g0728300	Similar to Cytochrome P450 CYP72A5
1.05	0.02	Os01g0728350	Similar to Cytochrome P450 CYP72A5
2.87	0.02	Os02g0113200	Similar to Cytochrome P450-like protein
1.29	0.02	Os08g0507000	Similar to Cyt-P450 monooxygenase
1.07	0.02	Os07g0229700	Similar to DNA-directed RNA polymerase I subunit 12
1.31	0.02	Os01g0681100	Similar to Dynamin-related protein 1B
1.04	0.02	Os04g0618500	Similar to Gamma-SNAP

1.18	0.02	Os09g0425200	Similar to Glycine-rich protein
1.08	0.02	Os09g0531900	Similar to Glycosyltransferase QUASIMODO1
1.09	0.02	Os02g0740400	Similar to GSDL-motif lipase
1.24	0.02	Os04g0562500	Similar to H0211B057 protein
1.1	0.02	Os04g0633300	Similar to H0613A104 protein
1.18	0.02	Os04g0664900	Similar to H1005F085 protein
1.06	0.02	Os08g0206500	Similar to HAP5 subunit of HAP complex
1.01	0.02	Os01g0827300	Similar to Laccase precursor
1.01	0.02	Os03g0811100	Similar to Magnesium-chelatase subunit chlD
1.16	0.02	Os07g0517500	Similar to mitochondrial protein
1.31	0.02	Os05g0276100	Similar to Na+/H+ exchangeing protein-like
1.05	0.02	Os09g0253000	Similar to NOI protein
1.07	0.02	Os08g0557100	Similar to Nucleic acid-binding protein precursor
1.09	0.02	Os02g0734300	Similar to Nudix hydrolase 18, mitochondrial precursor
1.01	0.02	Os06g0634300	Similar to Nudix hydrolase 2
1.1	0.02	Os09g0358400	Similar to OsD305
1.86	0.02	Os04g0523700	Similar to OSIGBa0153E02-OSIGBa0093I209 protein
1.11	0.02	Os01g0350200	Similar to P450
1.25	0.02	Os11g0661600	Similar to Peroxidase
1.44	0.02	Os07g0608900	Similar to Peroxisome assembly protein 10
1.21	0.02	Os03g0337500	Similar to Potassium transporter
1.4	0.02	Os07g0128800	Similar to PR1a protein
1.34	0.02	Os12g0555000	Similar to Probenazole-inducible protein PBZ1
1.31	0.02	Os12g0555200	Similar to Probenazole-inducible protein PBZ1
1.08	0.02	Os11g0226201	Similar to Protein kinase , expressed
1.34	0.02	Os01g0256500	Similar to Ramy1
1.11	0.02	Os01g0116900	Similar to Receptor kinase LRK10
1.37	0.02	Os06g0549300	Similar to reticuline oxidase
1.23	0.02	Os07g0158300	Similar to RNA binding protein
1.41	0.02	Os11g0208650	Similar to S-domain receptor-like protein kinase family-
1.59	0.02	Os03g0231700	Similar to squalene monooxygenase
1.25	0.02	Os10g0136500	Similar to SRK5 protein
1.13	0.02	Os01g0720600	Similar to Starch synthase IV
2.09	0.02	Os01g0337100	Similar to Terpene synthase 11
1.16	0.02	Os02g0754000	Similar to TLD
1.16	0.02	Os10g0514901	Similar to Transposon protein
1.1	0.02	Os10g0521000	Similar to TRE1 protein
1.01	0.02	Os08g0344600	Similar to Triose phosphate/phosphate translocator
1.06	0.02	Os03g0793600	Similar to type I inositol-1,4,5-trisphosphate 5-
1.49	0.02	Os06g0506600	Similar to Ubiquitin-conjugating enzyme E2-17 kDa 8
1.32	0.02	Os02g0437800	Similar to vacuolar protein-sorting protein 45
1.12	0.02	Os03g0111700	Similar to Valyl-tRNA synthetase
1.06	0.02	Os04g0599000	Similar to WAK53a - OsWAK receptor-like protein
1.56	0.02	Os04g0365100	Similar to Wall-associated kinase 4
1.34	0.02	Os09g0561450	Similar to Wall-associated kinase-like 1
1.26	0.02	Os01g0842801	Similar to WRKY transcription factor 56

1.78	0.02	Os12g0101600	Similar to WUSCHEL-related homeobox 3
1.03	0.02	Os12g0232300	Similar to ZCN20
1.05	0.02	Os08g0120000	Succinate dehydrogenase iron-protein subunit
1.14	0.02	Os04g0436100	Thioesterase superfamily
1.04	0.02	Os03g0767500	Thioredoxin domain 2 containing protein
2.16	0.02	Os09g0559600	Thioredoxin domain 2 containing protein
1.2	0.02	Os09g0442400	t-snare domain containing protein
1.01	0.02	Os05g0242133	Ubiquitin
1.73	0.02	Os11g0708500	Vitamin B6 biosynthesis protein
1.35	0.02	Os01g0972800	WRKY1
1.31	0.02	Os10g0464900	Zinc finger, RING/FYVE/PHD-type
1.09	0.03	Os03g0790700	Aldehyde oxidase-2
1.19	0.03	Os07g0625400	BTB/POZ fold domain containing protein
1.38	0.03	Os06g0702700	Butirosin biosynthesis, BtrG-like domain
1.19	0.03	Os06g0671300	Cytochrome P450
1.57	0.03	Os03g0147400	Divalent ion symporter
1.43	0.03	Os06g0127800	Dwarf and low-tillering; GAI-
1.04	0.03	Os01g0949700	Glutathione S-transferase, C-terminal
1.65	0.03	Os04g0474300	Glycoside hydrolase, family 1 protein
1.28	0.03	Os01g0860800	Glycoside hydrolase, family 17 protein
1	0.03	Os01g0601625	Leucine rich repeat, N-terminal
1.17	0.03	Os05g0426000	MtN3 and saliva related transmembrane protein
1.94	0.03	Os01g0816550	Non-protein coding transcript
1.04	0.03	Os03g0233900	Non-symbiotic hemoglobin 1
1.02	0.03	Os08g0320100	Nucleotide-binding, alpha-beta plait
1.32	0.03	Os12g0141500	Peptidase, trypsin-like serine and cysteine
1.01	0.03	Os04g0654600	Protein kinase, core
1.06	0.03	Os11g0557500	Protein kinase, core
1.18	0.03	Os09g0110300	Putative cyclase
1.76	0.03	Os03g0197300	RmlC-like jelly roll fold
1.52	0.03	Os05g0102000	SAM dependent carboxyl methyltransferase
1.67	0.03	Os02g0114200	Serine carboxypeptidase III precursor (EC 34165)
1.14	0.03	Os10g0112700	Serine/threonine protein kinase-related
1.19	0.03	Os02g0116900	Similar to 159 kDa subunit of RNA polymerase II
1.07	0.03	Os02g0503500	Similar to 3-oxoacyl-[acyl-carrier-protein] reductase
1.25	0.03	Os02g0465400	Similar to 7-dehydrocholesterol reductase
1.3	0.03	Os03g0769100	Similar to 9S ribosomal protein
1.6	0.03	Os03g0101000	Similar to Adenosine monophosphate binding protein 1
1.58	0.03	Os02g0218700	Similar to Allene oxide synthase
1.05	0.03	Os03g0861300	Similar to Aquaporin
1.2	0.03	Os07g0539900	Similar to Beta-1,3-glucanase-like protein
1.71	0.03	Os07g0654700	Similar to BLE2 protein
1.08	0.03	Os04g0559400	Similar to Branched-chain-amino-acid aminotransferase
1.07	0.03	Os01g0803600	Similar to cDNA, clone: J100035A04
1.15	0.03	Os10g0543400	Similar to Chitinase
1.16	0.03	Os02g0811800	Similar to Cinnamoyl-CoA reductase

1.02	0.03	Os03g0749300	Similar to Exoglucanase precursor
1	0.03	Os02g0618100	Similar to Glutaredoxin-C4, chloroplastic
1.1	0.03	Os02g0156000	Similar to H0201G082 protein
1.54	0.03	Os04g0456200	Similar to H0523F076 protein
1.38	0.03	Os04g0633200	Similar to H0613A101 protein
1.03	0.03	Os03g0286900	Similar to Low-temperature induced protein lt1012
1.1	0.03	Os09g0554000	Similar to Mitochondrial phosphate transporter
1.74	0.03	Os11g0126900	Similar to NAC domain transcription factor
1.28	0.03	Os07g0129500	Similar to Pathogenesis-related protein 1
1.03	0.03	Os10g0486200	Similar to Plastidic phosphate translocator-like protein1
1.24	0.03	Os07g0168000	Similar to Polyribonucleotide phophorylase
1.28	0.03	Os08g0529100	Similar to Proteasome subunit beta type 1
1.04	0.03	Os10g0547900	Similar to Short-chain dehydrogenase Tic32
1.01	0.03	Os05g0596600	Similar to SMC5 protein
1.38	0.03	Os04g0131850	Similar to sterol 3-beta-glucosyltransferase
1.05	0.03	Os08g0561700	Similar to Superoxide dismutase
1.54	0.03	Os10g0527400	Similar to Tau class GST protein 3
3.06	0.03	Os02g0817800	Similar to Telomere binding protein-1
2.01	0.03	Os08g0167800	Similar to Terpene synthase 10
1.13	0.03	Os06g0146250	Similar to WRKY transcription factor 73
1.03	0.03	Os01g0971700	Streptomyces cyclase/dehydrase
1.03	0.03	Os01g0597800	UDP-glucuronosyl/UDP-glucosyltransferase
1.08	0.03	Os05g0475300	VHS domain containing protein
1.29	0.03	Os06g0682800	Zinc finger, CCCH-type
1.11	0.04	Os10g0166600	Cytochrome P450
1.04	0.04	Os03g0108600	DEAD-like helicase, N-terminal
1.48	0.04	Os08g0180300	DEAD-like helicase, N-terminal
1.28	0.04	Os12g0154900	Germin-like protein precursor
1.48	0.04	Os01g0623600	Glycoside hydrolase, family 28 protein
1.48	0.04	Os02g0227600	Leucine-rich repeat, plant specific containing protein
1.06	0.04	Os04g0205200	NB-ARC
1.08	0.04	Os11g0661000	Pentatricopeptide repeat
1.09	0.04	Os10g0577800	Poly (ADP-ribose) polymerase, catalytic region
1.1	0.04	Os01g0116200	Protein kinase, core
1.52	0.04	Os12g0230600	Protein of unknown function DUF1685
1.33	0.04	Os02g0709800	RabGAP/TBC
1.06	0.04	Os01g0678600	Ribosomal protein S20
1.05	0.04	Os03g0452300	Ribosomal protein S5, bacterial-type
1.9	0.04	Os01g0348900	SalT gene product
1.1	0.04	Os01g0138300	Serine/threonine protein kinase-related
1.2	0.04	Os04g0368800	Serine/threonine protein kinase-related
1.4	0.04	Os11g0212900	Serine/threonine protein kinase-related
1.06	0.04	Os01g0273000	Similar to 26 proteasome complex subunit DSS1
1	0.04	Os03g0704000	Similar to 30S ribosomal protein S13
1	0.04	Os05g0178600	Similar to Auxin-responsive protein
1.29	0.04	Os04g0202700	Similar to Avr9/Cf-9 rapidly elicited protein 256

1.66	0.04	Os09g0464000	Similar to Carbonate dehydratase-like protein
1.1	0.04	Os10g0416500	Similar to Chitinase 1 precursor (EC 32114)
1.23	0.04	Os07g0275801	Similar to Chloroplast photosystem II reaction
1.17	0.04	Os11g0702100	Similar to Class III chitinase homologue
1.03	0.04	Os04g0311400	Similar to Cysteine proteinase 1 precursor
1.98	0.04	Os01g0187600	Similar to Cytokinin dehydrogenase 1 precursor
1.02	0.04	Os02g0128000	Similar to Cytosolic class I small heat shock protein 6
1.04	0.04	Os12g0194600	Similar to DNA binding protein
1.01	0.04	Os06g0552500	Similar to glucan endo-1,3-beta-glucosidase 7
1.63	0.04	Os01g0946700	Similar to Glucan endo-1,3-beta-glucosidase GV
1.38	0.04	Os04g0432100	Similar to GRAS family transcription factor
1	0.04	Os04g0459500	Similar to H0219H121 protein
1.33	0.04	Os02g0747500	Similar to HVA22-like protein e
1.04	0.04	Os03g0310800	Similar to Hypersensitive reaction associated Ca2+-
1.68	0.04	Os12g0560200	Similar to Lipoxygenase
1.12	0.04	Os03g0288000	Similar to Metallothionein
1.02	0.04	Os11g0675200	Similar to NB-ARC
2.07	0.04	Os12g0444800	Similar to O-methyltransferase ZRP4
1.03	0.04	Os04g0369600	Similar to OSIGBa0107E143 protein
1.68	0.04	Os01g0382400	Similar to Pathogenesis-related protein PRB1-2
1.28	0.04	Os02g0133200	Similar to Phosphatidylinositol transfer-like protein IV
1.19	0.04	Os06g0476200	Similar to Phosphoglucomutase precursor
1.25	0.04	Os12g0277500	Similar to RuBisCO subunit binding-protein alpha
1.09	0.04	Os12g0514000	Similar to Sorbitol transporter
1.7	0.04	Os10g0147200	Similar to Thaumatin-like protein
1.02	0.04	Os12g0116600	Similar to Transcription factor
1.13	0.04	Os03g0681400	Similar to Ubiquitin-conjugating enzyme E2-18 kDa
1.29	0.04	Os03g0820500	Similar to WCOR719
2.14	0.04	Os02g0121700	Terpenoid synthase
1.04	0.04	Os02g0571100	Terpenoid synthase
1.53	0.04	Os11g0474600	Terpenoid synthase
1.58	0.04	Os07g0454400	TonB box, conserved site
1.56	0.04	Os04g0627900	Translation initiation factor SUI1
1.71	0.04	Os05g0590100	Ubiquitin
1.58	0.04	Os03g0841600	UDP-glucuronosyl/UDP-glucosyltransferase
1.32	0.04	Os02g0682300	Zinc finger, RING/FYVE/PHD-type
1.11	0.05	Os06g0176300	2OG-(FeII) oxygenase
1.42	0.05	Os07g0543500	Armadillo-like helical
1.19	0.05	Os07g0500300	C2 calcium-dependent membrane targeting
1.03	0.05	Os06g0681200	Cupredoxin
1.3	0.05	Os05g0567300	GTP-binding protein, HSR1-related
2.05	0.05	Os01g0190500	IQ calmodulin-binding region
1.33	0.05	Os01g0901700	Monooxygenase, FAD-binding
1.02	0.05	Os11g0126100	Multi antimicrobial extrusion protein MatE
1.02	0.05	Os08g0387400	Similar to Cellulase
1.07	0.05	Os06g0569500	Similar to Ent-kaurene oxidase 1

1.17	0.05	Os09g0501850	Similar to FK506-binding protein 2-1 precursor
1.63	0.05	Os03g0129300	Similar to Glyceraldehyde-3-phosphate dehydrogenase
2.02	0.05	Os08g0151000	Similar to Myb-like DNA-binding domain
1.39	0.05	Os05g0513400	Similar to non-imprinted in Prader-Willi
1.78	0.05	Os09g0344500	Similar to O-methyltransferase ZRP4
1.19	0.05	Os04g0601800	Similar to Plastid protein
1.04	0.05	Os08g0112700	Similar to TAGL12 transcription factor
1.07	0.05	Os02g0678800	Similar to Transcription activator
1.39	0.05	Os01g0734800	UDP-glucuronosyl/UDP-glucosyltransferase
1.23	0.05	Os06g0125800	Zinc finger, RING/FYVE/PHD-type
2.17	0.05	Os02g0595900	Similar to high affinity nitrate transporter
2.1	0.05	Os01g0947000	Similar to Beta-1,3-glucanase precursor
2.62	0.05	Os12g0458100	Transferase

Annex 2 Function related with down-regulated genes, expression (log2FC), p-value, locus ID, and description of gene function in leaves of 18-day-old rice seedlings (*Oryza sativa* ssp. *japonica* cv. Nipponbare) after four days of iron excess exposure.

Log_2FC	p-value	Locus ID	Description
-2.83	0,03	Os02g0536400	Nucleotide-binding, alpha-beta plait.
-2.54	0,02	Os06g0141200	Similar to RNA-binding protein EWS.
-1.82	0	Os01g0279400	Major facilitator superfamily antiporter.
-1.77	0,01	Os04g0688200	Similar to Peroxidase (EC 1.11.1.7)
-1.66	0,01	Os07g0251900	Leucine-rich repeat, N-terminal domain containing protein.
-1.63	0	Os12g0141000	Conserved hypothetical protein.
-1.6	0,01	Os09g0314800	Similar to PERK1-like protein kinase.
-1.57	0	Os04g0223901	Dimethylaniline monooxygenase, N-oxide-forming
-1.53	0,02	Os01g0694000	Protein kinase, core domain containing protein.
-1.53	0	Os04g0223500	Dimethylaniline monooxygenase, N-oxide-forming.
-1.33	0	Os09g0424200	Glutamine amidotransferase class-I domain containing protein.
-1.33	0	Os11g0655900	Thioredoxin fold domain containing protein.
-1.32	0,03	Os04g0581600	Similar to UDP-glucose dehydrogenase.
-1.31	0.02	Os10g0497700	Similar to Phytochelatin synthetase.
-1.3	0	Os01g0326300	Haem peroxidase, plant/fungal/bacterial family protein.
-1.29	0.02	Os02g0240300	Similar to Class III peroxidase GvPx2b
-1.28	0,01	Os03g0103300	Similar to QLTG-3-1 protein.
-1.21	0	Os10g0521900	Peptidase S54, rhomboid domain containing protein.
-1.2	0	Os08g0163300	DNA polymerase delta, subunit 4 family protein.
-1.19	0	Os02g0770800	Similar to Nitrate reductase [NAD(P)H] (EC 1.7.1.2)
-1.18	0.03	Os04g0225100	3'-5' exonuclease domain containing protein.
-1.17	0	Os07g0443500	Molecular chaperone, heat shock protein, Hsp40, DnaJ
-1.16	0.03	Os04g0322700	Similar to OSIGBa0115K01-H0319F09.21 protein.
-1.15	0	Os11g0154500	No apical meristem
-1.13	0,01	Os08g0474000	Similar to AP2 domain containing protein RAP2.6
-1.11	0.05	Os09g0506000	Similar to Diphosphonucleotide phosphatase 1 precursor.
-1.11	0.05	Os11g0485200	ATPase, P-type, K/Mg/Cd/Cu/Zn/Na/Ca/Na/H-transporter family protein.
-1.08	0.04	Os08g0473600	Alpha-amylase isozyme 3E precursor
-1.06	0	Os01g0631200	Similar to Uroporphyrinogen III methyltransferase.
-1.06	0.04	Os01g0737600	Similar to OSIGBa0101A01.4 protein.
-1.06	0.03	Os02g0730000	Similar to Mitochondrial aldehyde dehydrogenase.
-1.05	0	Os03g0103100	Similar to Physical impedance induced protein.
-1.05	0.02	Os05g0128700	Similar to PH domain containing protein.
-1.04	0.04	Os07g0240200	Similar to Beta-1,3 glucanase precursor
-1.03	0	Os09g0565300	Similar to RING-finger protein.
-1.03	0.05	Os10g0552200	Plant lipid transfer protein and hydrophobic protein, helical
-1.02	0,02	Os02g0677300	Similar to CRT/DRE binding factor 1.
-1.02	0,02	Os05g0506000	Similar to MS5-like protein
-1.01	0.01	Os02g0636600	GRAM domain containing protein.
-1	0,03	Os05g0418000	GDP dissociation inhibitor protein OsGDI1.
-1	0,03	Os07g0574500	Ubiquitin domain containing protein.
-1	0	Os12g0538700	Similar to AT.I.24-1 protein

Annex 3 Number of significant occurrences of ABA responsive cis-regulatory elements in promoter (1 kbp upstream) of up-regulated genes in leaves of 18-day-old rice seedlings (*Oryza sativa* ssp. *japonica* cv. Nipponbare) after four days of iron excess exposure.fold-change (log2FC), locus ID and description of 21- ABADESI2, 26- ABRE2HVA22, 28-ABRE3HVA22, 30-ABREA2HVA1, 31-ABREATCONSENSUS, 32-ABREATRD22, 33-ABREAZMRAB28,- 34- BREBNNAPA, 35-ABREBZMRAB28, 36-ABRECE1HVA22, 39-ABREDISTBBNNAPA, 40-ABRELATERD1, 41-ABREMOTIFAOSOSEM, 42-BREMOTIFIIIOSRAB16B, 43-ABREMOTIFIOSRAB16B, 44-ABREOSRAB21, 45-ABRERATCAL, 46-ABRETAEM, 47-ABREZMRAB28, 50-ACGTABREMOTIFA2OSEM, and 51-ACGTABREMOTIFAOSOSEM. NBS – number of binding sites, NDCRE (number of different cis-regulatory elements).

Log_2FC	Locus_ID	Description	*Cis*-regulatory element code																			NBS	NDCRE
			21	26	28	30	31	32	33	34	35	36	39	40	41	42	43	44	45	47	50	51		
1.17	Os04g0690800	22 kDa protein of photosystem II.												-							1		1	**1**
1.01	Os11g0135400	60S acidic ribosomal protein P0.												-				1	-				1	**1**
1.09	Os03g0790700	Aldehyde oxidase-2.																1					1	**1**
1.8	Os05g0363100	Alpha/beta hydrolase family protein.												-				1					1	**1**
1.49	Os12g0431100	ATPase, AAA-type, core																1					1	**1**
1.71	Os05g0569900	B-block binding subunit of TFIIIC												-					-		1		1	**1**
1.19	Os07g0500300	C2 calcium-dependent membrane targeting										1											1	**1**
1.51	Os02g0621300	Fatty acid hydroxylase												-				1	-				1	**1**
1.19	Os06g0207000	Fumble												-				1					1	**1**
1	Os01g0692100	Glutathione S-transferase, C-terminal-like												-							1		1	**1**
2.17	Os04g0513900	Glycoside hydrolase, family 1 protein.												-				1					1	**1**
1.61	Os01g0296700	Glycoside hydrolase, family 3, N-terminal												-				1					1	**1**
1.03	Os12g0578500	Glycosyl transferase, family 8 protein.												-				1	-				1	**1**
1.31	Os01g0956200	Glycosyltransferase AER61, uncharacterized												-					-		1		1	**1**
1.5	Os05g0171900	Glyoxalase/bleomycin resistance protein/dioxygenase												-					-		1		1	**1**
1.27	Os04g0660100	Helix-loop-helix DNA-binding												-					-		1		1	**1**
1.01	Os08g0490000	Helix-loop-helix DNA-binding												-				1	-				1	**1**
1.46	Os02g0654100	Similar to Enoyl-CoA hydratase.												-							1		1	**1**
1.68	Os01g0571800	Lateral organ boundaries, LOB												-				1	-				1	**1**
1.48	Os02g0227600	Leucine-rich repeat, plant specific containing protein.												-				1					1	**1**
1.39	Os11g0655800	Lipase, class 3 family protein.	1																				1	**1**
1.01	Os04g0573000	Major facilitator superfamily MFS_1 protein.																1					1	**1**
1.19	Os01g0143800	Mitochondrial glycoprotein family protein.																1					1	**1**
1.54	Os12g0125800	Multi antimicrobial extrusion protein MatE family protein.																1					1	**1**
1.63	Os08g0255225	Non-protein coding gene.												-							1		1	**1**
1.64	Os01g0591500	Non-protein coding transcript.												-					-		1		1	**1**
2.5	Os09g0572000	Pathogenesis-related transcriptional factor and ERF												-				1	-				1	**1**

1.16	Os02g0290000	Pentatricopeptide repeat														1					1	**1**
1.18	Os05g0294600	Pentatricopeptide repeat											-				1	-				1	**1**
1.04	Os07g0249900	Peptidase M20 family protein.											-							1		1	**1**
1.15	Os02g0168700	Peptidyl-prolyl cis-trans isomerase, FKBP-type											-				1	-				1	**1**
1.02	Os03g0852800	Phosphoesterase family protein.											-					-		1		1	**1**
1.09	Os01g0361500	Phospholipid/glycerol acyltransferase											-				1					1	**1**
1.02	Os02g0114400	Phospholipid/glycerol acyltransferase															1	-				1	**1**
1.34	Os11g0679700	Phospholipid/glycerol acyltransferase					1						-					-				1	**1**
1.58	Os12g0563000	Phospholipid/glycerol acyltransferase											-							1		1	**1**
1.09	Os10g0577800	Poly															1					1	**1**
1.37	Os04g0613900	Potassium uptake protein, kup											-					-		1		1	**1**
1.56	Os03g0297800	Protein kinase, core											-					-		1		1	**1**
1.07	Os01g0164600	Protein phosphatase 2C-related											-							1		1	**1**
1.1	Os01g0830100	Pyridine nucleotide-disulphide oxidoreductase, NAD-binding region											-		1			-				1	**1**
1.03	Os12g0284000	Regulator of chromosome condensation, RCC1															1					1	**1**
1.48	Os07g0182000	Basic leucine zipper transcriptional activator.											-							1		1	**1**
1.09	Os01g0231800	RNA ligase/cyclic nucleotide phosphodiesterase											-		1							1	**1**
1.22	Os02g0707900	Rossmann-like alpha/beta/alpha sandwich fold											-					-		1		1	**1**
1.37	Os01g0901900	S1, RNA binding															1					1	**1**
1.9	Os01g0348900	SalT gene product											-					-		1		1	**1**
1.33	Os02g0202700	Serine acetyltransferase.											-							1		1	**1**
1.08	Os03g0390200	Serine/threonine-protein kinase SAPK1											-							1		1	**1**
1.12	Os04g0531900	Short-chain dehydrogenase/reductase SDR											-				1					1	**1**
1.43	Os01g0503400	Similar to															1					1	**1**
1.14	Os07g0108300	Similar to Alanine aminotransferase.											-					-		1		1	**1**
1.35	Os12g0503000	Similar to Allantoin permease.											-							1		1	**1**
1.66	Os12g0226900	Similar to Allyl alcohol dehydrogenase.											-							1		1	**1**
1.53	Os11g0195600	Similar to Amino acid carrier									1							-				1	**1**
1.14	Os07g0485400	Similar to asparaginyl-tRNA synthetase.											-					-	1			1	**1**
1.09	Os08g0532400	Similar to AT.I.24-7 protein.											-					-		1		1	**1**
1.25	Os10g0147400	Similar to Auxin influx carrier protein.											-							1		1	**1**
1	Os05g0178600	Similar to Auxin-responsive protein											-					-		1		1	**1**
1.2	Os07g0539900	Similar to Beta-1,3-glucanase-like protein.											-					-	1			1	**1**
1.95	Os03g0749100	Similar to Beta-glucanase.											-				1	-				1	**1**
1.23	Os07g0656200	Similar to Beta-glucosidase.									1											1	**1**
1.35	Os07g0124300	Similar to bZIP transcription factor family protein.											-					-		1		1	**1**
1.25	Os08g0498400	Similar to Caffeoyl-CoA 3-O-methyltransferase											-				1					1	**1**
2.04	Os01g0804100	Similar to cDNA, clone: J100035A04, full insert sequence.											-					-		1		1	**1**
1.16	Os04g0556400	Similar to Cis-zeatin O-glucosyltransferase 1											-					-	1			1	**1**

1.12	Os02g0194100	Similar to Citrate synthase											-							1		1	**1**
1.06	Os03g0201100	Similar to Cyclophilin-like protein PPIL3b.											-							1		1	**1**
1.01	Os06g0655100	Similar to D-3-phosphoglycerate dehydrogenase.															1					1	**1**
1.07	Os03g0740600	Similar to Deoxyhypusine synthase											-				1	-				1	**1**
1.85	Os05g0402900	Similar to EDGP.											-				1	-				1	**1**
1.24	Os05g0574600	Similar to Fatty acid elongase 1-like protein.											-				1	-				1	**1**
1.03	Os07g0148200	Similar to Flavonol 3-O-glucosyltransferase											-					-		1		1	**1**
2.21	Os02g0650900	Similar to Glutamate dehydrogenase 2											-					-		1		1	**1**
1.02	Os08g0126300	Similar to Glyceraldehyde-3-phosphate dehydrogenase											-				1	-				1	**1**
1.2	Os07g0602800	Similar to glycerophosphoryl diester phosphodiesterase.											-				1					1	**1**
1.18	Os09g0425200	Similar to Glycine-rich protein.											-					-		1		1	**1**
1.05	Os12g0632000	Similar to Glycine-rich RNA-binding protein 1						1					-									1	**1**
1.17	Os07g0412100	Similar to Granule-bound starch synthase Ib, chloroplast precursor											-				1	-				1	**1**
1.38	Os04g0432100	Similar to GRAS family transcription factor.															1					1	**1**
1.71	Os04g0310800	Similar to H0211A12.17 protein.															1					1	**1**
1.24	Os04g0562500	Similar to H0211B05.7 protein.															1	-				1	**1**
1.39	Os07g0542800	Similar to H0306B06.7 protein.											-					-		1		1	**1**
1.05	Os07g0111301	Similar to H0515C11.12 protein.						1					-					-				1	**1**
1.33	Os02g0547300	Similar to H0523F07.7 protein.											-							1		1	**1**
1.08	Os08g0546800	Similar to Heat stress transcription factor B-2b.											-					-		1		1	**1**
2.49	Os05g0237800	Similar to Histidine amino acid transporter.															1	-				1	**1**
1.34	Os01g0152700	Similar to Histone H2B											-				1	-				1	**1**
1.08	Os06g0103300	Similar to Homogentisate 1,2-dioxygenase											-				1					1	**1**
1.04	Os03g0310800	Similar to Hypersensitive reaction associated Ca2+binding protein.											-				1	-				1	**1**
1.03	Os07g0592600	Similar to Indole-3-acetic acid-amido synthetase GH3.3											-				1	-				1	**1**
1.18	Os04g0619000	Similar to L1332.9 protein.										1										1	**1**
1.11	Os07g0131500	Similar to lectin-like receptor kinase 7.											-					-		1		1	**1**
1.08	Os04g0583900	Similar to LHY protein.											-							1		1	**1**
1.12	Os05g0524300	Similar to Mitochondrial processing peptidase.											-				1					1	**1**
1.57	Os02g0258900	Similar to Molybdopterin biosynthesis CNX2 protein								1												1	**1**
1.59	Os07g0138200	Similar to NAC domain protein, IPR003441.											-							1		1	**1**
1.36	Os06g0287000	Similar to NBS-LRR type R protein, Nbs4-Pi.											-							1		1	**1**
1.39	Os08g0470200	Similar to Nectarin III.											-				1					1	**1**
1.24	Os04g0538400	Similar to Nodulin 21															1					1	**1**
1.18	Os04g0370800	Similar to OSIGBa0134J07.3 protein.											-					-		1		1	**1**
1.79	Os08g0189200	Similar to Oxalate oxidase															1					1	**1**
1.24	Os01g0844300	Similar to Peptidylprolyl isomerase.											-				1					1	**1**
1.19	Os04g0601800	Similar to Plastid protein.											-					-		1		1	**1**
1.38	Os02g0797500	Similar to Plastidic aspartate aminotransferase.									1		-					-				1	**1**

1.32	Os01g0609200	Similar to Pleiotropic drug resistance protein 3.											-					-		1		1	**1**
2.31	Os05g0575000	Similar to predicted protein.											-					-		1		1	**1**
1.19	Os09g0511700	Similar to Prunasin hydrolase isoform PH C precursor										1						-				1	**1**
1.11	Os01g0116900	Similar to Receptor kinase LRK10.											-					-		1		1	**1**
1.71	Os05g0463000	Similar to Receptor protein kinase-like protein.											-				1					1	**1**
1.07	Os03g0773700	Similar to Receptor-like protein kinase 2.											-					-		1		1	**1**
1.18	Os10g0389200	Similar to Red chlorophyll catabolite reductase [Oryza sativa											-					-		1		1	**1**
1.18	Os05g0427300	Similar to RNA binding protein											-				1					1	**1**
1.19	Os02g0723600	Similar to RNA polymerase Rpb3/Rpb11 dimerisation											-							1		1	**1**
1.12	Os01g0928700	Similar to Serine palmitoyltransferase.											-				1	-				1	**1**
1.14	Os05g0263100	Similar to SHR5-receptor-like kinase											-					-	1			1	**1**
1.07	Os02g0678800	Similar to Transcription activator.											-				1					1	**1**
1.73	Os11g0175700	Similar to Transcription factor PCF3											-				1	-				1	**1**
1.03	Os11g0549900	Similar to tubulin alpha-6 chain.											-					-		1		1	**1**
1.12	Os07g0680000	Similar to Vacuolar sorting receptor 1 precursor			1																	1	**1**
3.81	Os02g0112900	Similar to Viroid RNA-binding protein															1					1	**1**
1.03	Os05g0397650	Similar to Zinc finger, RING-type.											-					-	1			1	**1**
1.03	Os01g0971700	Streptomyces cyclase/dehydrase family protein.															1					1	**1**
1.29	Os01g0358300	Tetratricopeptide-like helical											-				1					1	**1**
1.04	Os03g0767500	Thioredoxin domain 2 containing protein.											-							1		1	**1**
1.01	Os01g0775300	TRAF-type															1					1	**1**
1.56	Os04g0627900	Translation initiation factor SUI1											-					-		1		1	**1**
1.18	Os01g0144200	Vacuolar import and degradation protein Vid24															1					1	**1**
1.02	Os11g0610700	WD40 repeat-like											-				1					1	**1**
1.15	Os03g0626600	Zinc finger, LIM-type															1	-				1	**1**
1.15	Os03g0650900	Zinc finger, RING/FYVE/PHD-type											-				1					1	**1**
1.06	Os04g0648500	Zinc finger, RING/FYVE/PHD-type											-					-		1		1	**1**
1	Os08g0384900	Zinc finger, RING/FYVE/PHD-type											-							1		1	**1**
1.14	Os04g0182200	2OG-Fe											-					2				2	**1**
1.02	Os05g0317200	AMP-dependent synthetase and ligase																2				2	**1**
1.32	Os06g0286228	Cupredoxin									1		-				1					2	**2**
1.03	Os10g0123200	Cyclin-like F-box											-					2				2	**1**
1.74	Os07g0567400	Cytochrome c region					1						-							1		2	**2**
1.52	Os02g0187000	Cytochrome P450 family protein.											-					2				2	**1**
1.11	Os10g0166600	Cytochrome P450 family protein.											-				1			1		2	**2**
1.06	Os01g0626400	DNA-binding protein WRKY2-like											-					2				2	**1**
1.4	Os06g0570100	Ent-kaurene oxidase											-					-		2		2	**1**
1.67	Os11g0649900	Exo70 exocyst complex subunit family protein.					1						-					-		1		2	**2**
1.29	Os06g0549600	FAD-linked oxidase, FAD-binding, subdomain 2									1		-							1		2	**2**

1.21	Os11g0495950	FAD-linked oxidase, FAD-binding, subdomain 2															2				2	**1**
1.46	Os01g0876300	F-box associated type 1											-				1	-		1		2	**2**
1.68	Os07g0592000	Gibberellin regulated protein family protein.											-					2				2	**1**
1.02	Os05g0539400	Glycoside hydrolase, family 35 protein.																2				2	**1**
1.3	Os05g0567300	GTP-binding protein, HSR1-related																2				2	**1**
1.38	Os05g0305700	Homeodomain-like containing protein.																2				2	**1**
1.9	Os11g0696900	Laccase											-					2				2	**1**
1.18	Os12g0215950	Leucine-rich repeat, N-terminal											-					2				2	**1**
1.16	Os12g0632700	Malate dehydrogenase, glyoxysomal precursor					1						-					-		1		2	**2**
1.07	Os01g0684900	Multi antimicrobial extrusion protein MatE family protein.											-					2				2	**1**
1.2	Os07g0484700	Myb transcription factor											-					2				2	**1**
1.52	Os05g0261001	Non-protein coding gene.					1						-					-		1		2	**2**
1.94	Os01g0816550	Non-protein coding transcript.			1								-					-		1		2	**2**
1.11	Os01g0956600	Nucleotide-binding, alpha-beta plait																2				2	**1**
1.44	Os07g0239600	Pentatricopeptide repeat											-					2				2	**1**
1.37	Os08g0481000	Pentatricopeptide repeat											-					2				2	**1**
1.26	Os10g0181200	Pentatricopeptide repeat											-					2				2	**1**
1.37	Os10g0451900	Peptidase S8 and S53, subtilisin, kexin, sedolisin											-					2				2	**1**
1.38	Os02g0751600	Peptidyl-prolyl cis-trans isomerase, FKBP-type																2				2	**1**
1.32	Os12g0263600	Pinoresinol-lariciresinol reductase TH1.																2				2	**1**
1.53	Os02g0694800	Protein kinase											-					2				2	**1**
1.06	Os11g0557500	Protein kinase, core											-					2				2	**1**
2.29	Os04g0614500	Pyridoxal phosphate-dependent transferase, major region, subdomain1											-					2				2	**1**
1	Os11g0216000	Pyruvate kinase family protein.																2				2	**1**
1.16	Os10g0512500	RNA-binding, CRM domain											-				1			1		2	**2**
1.53	Os03g0826700	SAM											-					2				2	**1**
1.11	Os04g0202300	Serine/threonine protein kinase-related											-					2				2	**1**
1.26	Os03g0243300	Similar to 26S proteasome non-ATPase regulatory subunit 4											-				2					2	**1**
1.58	Os02g0218700	Similar to Allene oxide synthase					1						-							1		2	**2**
1.66	Os09g0464000	Similar to Carbonate dehydratase-like protein.											-					2				2	**1**
1.08	Os10g0546600	Similar to Chloroplast carotenoid epsilon-ring hydroxylase.											-				1	-		1		2	**2**
1.25	Os10g0194200	Similar to Cinnamyl alcohol dehydrogenase											-				1	-	1			2	**2**
1.03	Os02g0799000	Similar to DNA-binding protein phosphatase 2C.					1						-					-		1		2	**2**
1.14	Os10g0124600	Similar to DnaJ											-					2				2	**1**
1.05	Os03g0776900	Similar to DNAJ protein-like.																2				2	**1**
1.58	Os06g0486900	Similar to Formate dehydrogenase, mitochondrial precursor						1					-					-	1			2	**2**
1.04	Os04g0618500	Similar to Gamma-SNAP																2				2	**1**
2.5	Os02g0755900	Similar to Glucosyltransferase											-					2				2	**1**
1.22	Os01g0949750	Similar to Glutathione S-transferase GST 28					1						-							1		2	**2**

1.03	Os04g0202500	Similar to H0512B01.11 protein.											-					2				2	**1**
1.01	Os01g0133400	Similar to Hexose transporter											-					2				2	**1**
1.33	Os02g0747500	Similar to HVA22-like protein e											-					2				2	**1**
1.01	Os03g0811100	Similar to Magnesium-chelatase subunit chlD, chloroplast precursor											-				1	-		1		2	**2**
1.05	Os01g0829800	Similar to Malate dehydrogenase precursor											-					2				2	**1**
1.5	Os03g0838800	Similar to nucleic acid binding protein.											-					2				2	**1**
1.63	Os04g0430900	Similar to OSIGBa0160I14.4 protein.																2				2	**1**
1.11	Os01g0350200	Similar to P450.											-					2				2	**1**
1.04	Os08g0388900	Similar to para-hydroxybenzoate--polyprenyltransferase.											-					2				2	**1**
1.19	Os06g0476200	Similar to Phosphoglucomutase precursor											-					2				2	**1**
1.21	Os03g0337500	Similar to Potassium transporter.					1						-					-		1		2	**2**
1	Os08g0254500	Similar to Preprotein translocase secY subunit, chloroplast precursor											-				1	-		1		2	**2**
1.3	Os12g0145200	Similar to Protein MONOCULM 1.											-				1	-	1			2	**2**
2.46	Os02g0572300	Similar to RING-H2 finger protein ATL3B.											-					2				2	**1**
1.7	Os11g0218200	Similar to RNApol24.											-					2				2	**1**
1.41	Os11g0208650	Similar to S-domain receptor-like protein kinase family-3.																2				2	**1**
1.73	Os03g0197200	Similar to Sorbitol transporter.											-				1	-		1		2	**2**
1.25	Os10g0136500	Similar to SRK5 protein																2				2	**1**
1.13	Os01g0720600	Similar to Starch synthase IV.											-					2				2	**1**
2.78	Os10g0525600	Similar to Tau class GST protein 3.											-					2				2	**1**
2.01	Os08g0167800	Similar to Terpene synthase 10.											-					2				2	**1**
1.05	Os01g0187900	Similar to Transcription factor MYBS2.							1				-					-		1		2	**2**
1.1	Os10g0521000	Similar to TRE1 protein																2				2	**1**
1.04	Os11g0644800	Similar to Tyrosine/nicotianamine aminotransferases family protein											-					2				2	**1**
1	Os01g0867600	Similar to UDP-glucose:sterol glucosyltransferase											-					2				2	**1**
1.41	Os01g0965400	Similar to Uridylate kinase					1						-							1		2	**2**
1.7	Os03g0758950	Similar to WRKY58															2	-				2	**1**
1.34	Os07g0550600	Transferase family protein.											-					2				2	**1**
1.11	Os05g0592600	Translation initiation factor 2 related																2				2	**1**
1.2	Os09g0442400	t-snare																2				2	**1**
1.2	Os04g0206600	UDP-glucuronosyl/UDP-glucosyltransferase family protein.											-					2				2	**1**
1.01	Os05g0405900	WD40 repeat-like																2				2	**1**
1.02	Os03g0717600	Zinc finger, C2H2-type matrin																2				2	**1**
1.07	Os05g0411200	Adrenodoxin reductase family protein.											-	1				-		1	1	3	**3**
1.53	Os03g0225900	Allene oxide synthase.											-					3				3	**1**
1.13	Os12g0467700	ATPase, AAA-type, core											-	1						1	1	3	**3**
1.16	Os06g0726400	Branching enzyme-I precursor					1						-					-	1	1		3	**3**
1.23	Os01g0385400	C4-dicarboxylate transporter/malic acid transport protein family											3					-				3	**1**
1.06	Os04g0320100	Coenzyme F420 hydrogenase/dehydrogenase beta subunit					1						-				1			1		3	**3**

1.92	Os02g0569400	Cytochrome P450 family protein.											-					3				3	**1**
1.2	Os06g0501900	Cytochrome P450 family protein.											-					3				3	**1**
1.92	Os10g0513900	Cytochrome P450 family protein.																3				3	**1**
1.03	Os10g0525200	Cytochrome P450 family protein.											-					2		1		3	**2**
1.19	Os07g0607700	Di-trans-poly-cis-decaprenylcistransferase family protein.					1						-					-	1	1		3	**3**
1.26	Os01g0773600	Glycoside hydrolase, family 47 protein.					1	1					-							1		3	**3**
1.47	Os08g0253800	Glycosyl transferase, family 2				1	1						-					-		1		3	**3**
1.4	Os04g0538900	Glyoxalase/bleomycin resistance protein/dioxygenase					1	1					-							1		3	**3**
2.27	Os04g0677300	Harpin-induced 1											-					2		1		3	**2**
1	Os04g0667600	Heavy metal transport/detoxification protein											-					2	1			3	**2**
1.04	Os07g0274700	HvB12D protein											-					3				3	**1**
1.35	Os06g0176700	Isopenicillin N synthase family protein.											-					2		1		3	**2**
1.13	Os07g0694700	L-ascorbate peroxidase.							1				-				1	-	1			3	**3**
1.58	Os01g0881900	Leucine-rich repeat, cysteine-containing containing protein.											-					2		1		3	**2**
1.34	Os10g0558800	Major facilitator superfamily protein.											3					-				3	**1**
1.22	Os11g0206600	Mitochodrial transcription termination factor-related family protein.											3					-				3	**1**
1.11	Os03g0606200	Mitochondrial ATP synthase 6 KD subunit.											-					2	1			3	**2**
1.33	Os01g0901700	Monooxygenase, FAD-binding					1						-					-	1	1		3	**3**
1.16	Os10g0345100	Multi antimicrobial extrusion protein MatE family protein.											-					2		1		3	**2**
1.4	Os10g0576900	NAD					1						-				1	-		1		3	**3**
1.01	Os11g0588600	NB-ARC					1						-					-	1	1		3	**3**
1.78	Os10g0414000	No apical meristem											-					3				3	**1**
1.3	Os10g0407000	Pectin lyase fold/virulence factor						1					-					2				3	**2**
1.07	Os04g0668700	Phosphatidylinositol 3- and 4-kinase, catalytic											-				1	2				3	**2**
1.11	Os04g0469500	Phosphofructokinase family protein.					1						-				1			1		3	**3**
1.16	Os05g0560300	Protein kinase, core					1						-				1			1		3	**3**
1.5	Os12g0613600	Remorin, C-terminal region											-	1				-		1	1	3	**3**
1.05	Os03g0452300	Ribosomal protein S5, bacterial-type											3					-				3	**1**
1.76	Os03g0197300	RmlC-like jelly roll fold											-				1	2				3	**2**
1.07	Os07g0134600	Serine/threonine protein kinase											-				1	2				3	**2**
1.1	Os09g0356200	Serine/threonine protein kinase											-	1						1	1	3	**3**
1.14	Os10g0518800	Serine/threonine protein kinase											-					2		1		3	**2**
1.61	Os10g0468500	Serine/threonine protein kinase-related					1						-				1	-		1		3	**3**
1.02	Os03g0129100	Seven transmembrane protein MLO2.											-					3				3	**1**
2	Os02g0107900	Similar to ABC transporter family, cholesterol/phospholipid flippase.							1				-				1	-	1			3	**3**
1.31	Os09g0572400	Similar to Abcf2-prov protein.					1	1					-					-		1		3	**3**
1.6	Os03g0101000	Similar to Adenosine monophosphate binding protein 1 AMPBP1.					1						-					-	1	1		3	**3**
1.58	Os07g0281800	Similar to Aldehyde oxidase-2.											-	1						1	1	3	**3**
1.08	Os08g0244500	Similar to Beta-1,3-glucanase-like protein.					1						-					-	1	1		3	**3**

1.24	Os06g0184000	Similar to BHLH transcription factor.											3								3	**1**
1.32	Os07g0525900	Similar to Chalcone synthase.					1						-					-	1	1		3	**3**
1	Os10g0471300	Similar to Cyanate lyase											-					2	1			3	**2**
1.34	Os01g0968800	Similar to Dehydration responsive element binding protein 1F											3					-				3	**1**
1.13	Os01g0874800	Similar to DNA polymerase I.					1						-					-	1	1		3	**3**
1.16	Os12g0497300	Similar to DNA repair protein RAD51 homolog.					1						-					-	1	1		3	**3**
1.86	Os08g0141400	Similar to External rotenone-insensitive NADPH dehydrogenase.											-					2		1		3	**2**
1.15	Os07g0673200	Similar to F22D16.14 protein											-				1	2				3	**2**
1.05	Os02g0205500	Similar to Fatty acid elongase 1.											-	1						1	1	3	**3**
1.15	Os10g0408700	Similar to GAMYB-binding protein					1						-					-	1	1		3	**3**
1.63	Os01g0946700	Similar to Glucan endo-1,3-beta-glucosidase GV					1						-				1			1		3	**3**
1.2	Os11g0588300	Similar to Glutathione transferase AtGST 10											3					-				3	**1**
1.14	Os04g0209200	Similar to Glutathione-conjugate transporter AtMRP4.																3				3	**1**
1.81	Os10g0439800	Similar to H0813E03.1 protein.					1						-				1	-		1		3	**3**
1.27	Os09g0474300	Similar to Heat-shock protein precursor.											-				1	2				3	**2**
1.46	Os08g0246950	Similar to Heat-shock protein.					1						-					-	1	1		3	**3**
1.96	Os07g0529000	Similar to Isocitrate lyase					1	1					-					-		1		3	**3**
1.89	Os05g0311801	Similar to Isopentenyl transferase IPT7.					1	1					-							1		3	**3**
3.54	Os01g0842400	Similar to Laccase											-				1	2				3	**2**
1.16	Os09g0507300	Similar to L-ascorbate oxidase precursor																3				3	**1**
1.26	Os08g0477100	Similar to Latex allergen.					1						-				1			1		3	**3**
1.06	Os03g0638200	Similar to Major facilitator superfamily protein, expressed.											-					2		1		3	**2**
1.6	Os01g0816100	Similar to NAC domain protein.						1					-					2				3	**2**
1.01	Os06g0634300	Similar to Nudix hydrolase 2											-					3				3	**1**
1.36	Os03g0643300	Similar to Ornithine-oxo-acid transaminase.											3					-				3	**1**
1.52	Os10g0413600	Similar to OSIGBa0134P10.11 protein.											3					-				3	**1**
1.67	Os12g0638200	Similar to Peptide transporter.					1	1					-							1		3	**3**
1.44	Os07g0608900	Similar to Peroxisome assembly protein 10							1				-				1	-	1			3	**3**
1.06	Os04g0628100	Similar to Polyubiquitin.											-					2		1		3	**2**
1.02	Os11g0141000	Similar to PP2A regulatory subunit-like protein.											3					-				3	**1**
1.02	Os01g0295700	Similar to Protein phosphatase-2C.											-					3				3	**1**
1.25	Os03g0238600	Similar to Purple acid phosphatase.											-				1	2				3	**2**
1.26	Os01g0781200	Similar to Rust resistance protein.											3									3	**1**
1.26	Os02g0754100	Similar to S1 self-incompatibility locus-linked pollen G211 protein.											-				1	2				3	**2**
2.07	Os05g0433100	Similar to Serine/threonine-protein kinase SAPK7.											-					2	1			3	**2**
1.29	Os08g0176900	Similar to Transcription factor HBP-1b							1				-				1	-	1			3	**3**
1.01	Os01g0655300	Similar to Trithorax 4											-					2		1		3	**2**
1.49	Os01g0962300	Similar to Vacuolar ATP synthase 16 kDa proteolipid subunit					1						-				1	-		1		3	**3**
1.08	Os01g0246700	Similar to WRKY transcription factor 1.											3					-				3	**1**

1.05	Os08g0120000	Succinate dehydrogenase iron-protein subunit					1							-					-	1	1		3	**3**
1.62	Os09g0532000	TonB box, conserved site												-					3				3	**1**
1.08	Os11g0137500	Transcription factor TFE/TFIIEalpha, HTH domain												-					3				3	**1**
2.62	Os12g0458100	Transferase family protein.												3									3	**1**
1.45	Os01g0195500	Translation initiation factor SUI1												3									3	**1**
1.13	Os03g0405100	Ubiquinone biosynthesis protein COQ9					1	1						-					-		1		3	**3**
1.7	Os01g0511100	UspA					1							-					-	1	1		3	**3**
1.26	Os01g0311400	Zinc finger, RING/FYVE/PHD-type												-	1						1	1	3	**3**
1.2	Os02g0539200	Zinc finger, RING/FYVE/PHD-type												-	1				-		1	1	3	**3**
1.32	Os02g0682300	Zinc finger, RING/FYVE/PHD-type												-					2		1		3	**2**
1.31	Os10g0464900	Zinc finger, RING/FYVE/PHD-type												-					3				3	**1**
1.34	Os06g0128700	Zinc finger, RING-type												-	1						1	1	3	**3**
1.69	Os07g0162400	Alpha/beta hydrolase fold-3									1			-					2	1			4	**3**
2.78	Os07g0419100	Cytochrome P450 family protein.				1	1							-				1	-		1		4	**4**
1.05	Os10g0515900	Cytochrome P450 family protein.												3					-		1		4	**2**
1.29	Os05g0247100	Glycoside hydrolase, family 18 protein.												-				1	3				4	**2**
1.12	Os08g0374600	Molecular Function: protein kinase activity												-					4				4	**1**
1.38	Os04g0546800	Pathogenesis-related transcriptional factor and ERF												-	1				-	1	1	1	4	**4**
1.41	Os08g0191900	Pentatricopeptide repeat					1							-					2		1		4	**3**
1.12	Os10g0477200	Pentatricopeptide repeat												-				1	3				4	**2**
1.32	Os12g0141500	Peptidase, trypsin-like serine and cysteine												3							1		4	**2**
1.12	Os01g0747400	Protein kinase, core												3					-		1		4	**2**
1.57	Os07g0139000	Putative zinc finger CCCH domain-containing protein 48.					1							-				1	-		2		4	**3**
1.19	Os02g0116900	Similar to 15.9 kDa subunit of RNA polymerase II.												-				1	2	1			4	**3**
1.01	Os02g0817700	Similar to 3-ketoacyl-CoA thiolase												4									4	**1**
2.29	Os04g0389800	Similar to Acetohydroxyacid synthase.												-					3		1		4	**2**
1.08	Os05g0194500	Similar to ANAC075.												-				1	2	1			4	**3**
1.17	Os04g0630900	Similar to Anthocyanidin reductase.					1							-				1	-	1	1		4	**4**
1.2	Os02g0526400	Similar to ATP-dependent Clp protease ATP-binding subunit.												3				1	-				4	**2**
1.1	Os09g0416800	Similar to CCR4-NOT transcription complex subunit 7					1							-				1	-	1	1		4	**4**
3.29	Os05g0399300	Similar to Chitinase.												3					-		1		4	**2**
1.34	Os01g0951700	Similar to Cytochrome P450 CYP94E4.												3				1	-				4	**2**
2.87	Os02g0113200	Similar to Cytochrome P450-like protein.						1						3					-				4	**2**
1.05	Os06g0684000	Similar to FAD-dependent pyridine nucleotide-disulphide oxidoreductase												3					-		1		4	**2**
1.93	Os05g0367800	Similar to Luminal binding protein 2 precursor												-					4				4	**1**
1.22	Os04g0679800	Similar to RNA-binding protein-like protein.					1							-				2	-		1		4	**3**
1.15	Os04g0405300	Similar to Stem secoisolariciresinol dehydrogenase						1						3					-				4	**2**
1.05	Os08g0561700	Similar to Superoxide dismutase.												-				1	2	1			4	**3**

1.65	Os12g0629300	Similar to Thaumatin-like protein.											-					4				4	**1**
2.77	Os01g0734000	Similar to WRKY DNA binding protein.											-					3		1		4	**2**
1.5	Os03g0284800	Spo11/DNA topoisomerase VI, subunit A family protein.					1						-			1	1			1		4	**4**
1.05	Os07g0614600	Transmembrane receptor, eukaryota					1						-					2		1		4	**3**
1.76	Os06g0578700	von Willebrand factor, type A											-					4				4	**1**
1.07	Os12g0596800	Zinc finger, LIM-type											3					-	1			4	**2**
1.06	Os03g0188200	Zinc finger, RING/FYVE/PHD-type											3				1	-				4	**2**
1.63	Os04g0511200	EFA27 for EF hand, abscisic acid, 27kD.											3					2				5	**2**
1.13	Os02g0530100	Heavy metal transport/detoxification protein						1					3					-		1		5	**3**
1.33	Os01g0138900	Mandelate racemase/muconate lactonizing enzyme family protein.											-				1	3		1		5	**3**
1.76	Os12g0181900	Pentatricopeptide repeat											3					2				5	**2**
1.13	Os02g0168100	Similar to 4-hydroxyphenylpyruvate dioxygenase					1						-					2	1	1		5	**4**
1.46	Os03g0663201	Similar to cDNA clone:J033060E19, full insert sequence.					1						-					2	1	1		5	**4**
1.13	Os09g0467200	Similar to Glutathione S-transferase GST 23											3					2				5	**2**
1.31	Os05g0276100	Similar to Naقي exchangeing protein-like											3					2				5	**2**
1.68	Os02g0705400	Similar to Pathogen induced protein 2-4.					1						-					3		1		5	**3**
1.08	Os07g0633200	Similar to SC35-like splicing factor SCL30a, 30a kD.											-				1	3		1		5	**3**
1.61	Os01g0615100	Similar to Substilin /chymotrypsin-like inhibitor											3					2				5	**2**
1.59	Os01g0253900	Similar to triacylglycerol lipase.						1					3					-		1		5	**3**
1.79	Os03g0180900	Tify											5					-				5	**1**
1.02	Os08g0534400	Transcription factor Pcc1					1						-				1	2		1		5	**4**
1.2	Os03g0679000	Vacuolar import and degradation protein Vid24											-					3	1	1		5	**3**
1.06	Os12g0100500	Alpha/beta hydrolase family protein.											3	1						1	1	6	**4**
1.39	Os03g0251350	Histone-fold											4					2				6	**2**
1.52	Os12g0230600	Os12g0230600					1						-				1	2	1	1		6	**5**
2.85	Os03g0830400	PGPS/D12.											3					2		1		6	**3**
2.37	Os10g0491000	Plant Basic Secretory Protein family protein.					2	2					-							2		6	**3**
1.18	Os09g0110300	Putative cyclase family protein.											3	1				-		1	1	6	**4**
1.85	Os12g0268000	Similar to Cytochrome P450 71A1											3					3				6	**2**
1.02	Os04g0180400	Similar to Cytochrome P450 CYP99A1											3					3				6	**2**
1.89	Os07g0635500	Similar to Cytochrome P450.											4					2				6	**2**
1.04	Os05g0562300	Similar to DnaJ-like protein.											3					2		1		6	**3**
1.07	Os06g0569500	Similar to Ent-kaurene oxidase 1											4					2				6	**2**
1.11	Os03g0832600	Similar to Galactokinase											4				1	-		1		6	**3**
1.06	Os12g0176800	Similar to Heterochromatin protein											4					2				6	**2**
1.39	Os03g0626000	Similar to IBR											3					2		1		6	**3**
1.08	Os03g0710500	Similar to Luminal binding protein.											3	1				-		1	1	6	**4**
1.09	Os04g0607150	Similar to OSIGBa0113I13.10 protein.											3					2		1		6	**3**

1.53	Os08g0485400	Similar to Oxidoreductase.											3				1	2				6	**3**
1.2	Os12g0291100	Similar to Petunia ribulose 1,5-bisphosphate carboxylase small sub.					2						-					2		2		6	**3**
1.14	Os04g0518400	Similar to Phenylalanine ammonia-lyase											3					2		1		6	**3**
1.59	Os07g0127500	Similar to PR-1a pathogenesis related protein											4					2				6	**2**
2.04	Os08g0400000	Similar to Puromycin-sensitive aminopeptidase					1						-				1	2	1	1		6	**5**
1.68	Os03g0829200	Similar to Soluble epoxide hydrolase.											3					3				6	**2**
1.54	Os07g0182100	Similar to Tryptophan synthase alpha chain.											3					2		1		6	**3**
1.23	Os05g0387200	Similar to UDP-sulfoquinovose synthase, chloroplast precursor					1						-					3	1	1		6	**4**
1.31	Os06g0706600	Similar to wall-associated kinase 3.											3					3				6	**2**
1.43	Os05g0588800	Similar to Yarrowia lipolytica chromosome D						1					-				1	2	2			6	**4**
1.05	Os01g0593100	Similar to ZCW7.											4							2		6	**2**
1.28	Os03g0724300	Tyrosine protein kinase											3					3				6	**2**
1	Os11g0175500	Zinc finger, RING/FYVE/PHD-type					1						3				1	-		1		6	**4**
1.41	Os12g0197400	AIG1											3				1	2		1		7	**4**
1.69	Os12g0580400	Amino acid/polyamine transporter I family protein.						1					3				1	-	1	1		7	**5**
1.76	Os05g0247500	Glycoside hydrolase, family 18 protein.											3				1	3				7	**3**
1.05	Os01g0954000	NADPH-dependent FMN reductase family protein.											4					2		1		7	**3**
1.3	Os06g0618000	Nse4											3				1	3				7	**3**
1.01	Os03g0844000	Pentatricopeptide repeat											3					4				7	**2**
1.72	Os12g0557800	Pentatricopeptide repeat											3				1	3				7	**3**
1.11	Os05g0163700	Similar to Acyl-coenzyme A oxidase 4, peroxisomal						1					3					3				7	**3**
1.2	Os02g0764100	Similar to AP2 domain containing protein RAP2.8					1						3					-	1	2		7	**4**
1.55	Os09g0463900	Similar to DNA binding protein.					1						3			1	1	-		1		7	**5**
1.67	Os01g0276300	Similar to Group 3 late embryogenesis abundant protein											-	1				3		2	1	7	**4**
1.98	Os04g0561500	Similar to Prolyl endopeptidase											4					2		1		7	**3**
1	Os05g0438500	Similar to Soluble inorganic pyrophosphatase											3					3		1		7	**3**
2.41	Os07g0218200	Similar to terpene synthase 7.					1						-				1	2	2	1		7	**5**
1.16	Os10g0514901	Similar to Transposon protein.											3					2		2		7	**3**
1.16	Os05g0198200	Thioredoxin fold											4					3				7	**2**
1.27	Os01g0180800	Heat shock protein Hsp70 family protein.											3					4		1		8	**3**
1.26	Os05g0163900	Helix-loop-helix DNA-binding					1						3				1	2		1		8	**5**
1.26	Os01g0876400	Sad1/UNC-like, C-terminal											4					3	1			8	**3**
1.76	Os10g0567100	Similar to Chlorophyll b synthase											4					3		1		8	**3**
1.01	Os06g0552500	Similar to glucan endo-1,3-beta-glucosidase 7.											6					-		2		8	**2**
1	Os04g0459500	Similar to H0219H12.1 protein.											4				1	3				8	**3**
1.01	Os01g0246400	Similar to Low molecular mass early light-inducible protein HV90					1						-				3	2		2		8	**4**
1.1	Os09g0554000	Similar to Mitochondrial phosphate transporter.											3				1	2		2		8	**4**
1.39	Os03g0188500	Glutelin family protein.											3				2	2		2		9	**4**
1.17	Os01g0735400	Similar to Anthocyanidin 5,3-O-glucosyltransferase.					1						3				1	2		2		9	**5**

2.58	Os02g0749700	Similar to cDNA, clone: J065097H05, full insert sequence.											3				4	2				9	**3**
1.46	Os10g0146901	Similar to electron transporter/ thiol-disulfide exchange											6					2		1		9	**3**
1.23	Os01g0199300	Similar to lachrymatory factor synthase.											4	1			2	-		1	1	9	**5**
1.34	Os01g0256500	Similar to Ramy1.					1						4					2	1	1		9	**5**
1.29	Os03g0820500	Similar to WCOR719.					1	1					3					3		1		9	**5**
1.07	Os11g0160100	Zinc finger, RING/FYVE/PHD-type					2	1					3							3		9	**4**
1.49	Os07g0587500	Armadillo-like helical		1									3					5		1		10	**4**
1.5	Os08g0150700	Cyclin-like F-box											4				1	2		3		10	**4**
1.98	Os01g0187600	Similar to Cytokinin dehydrogenase 1 precursor											5					3		2		10	**3**
1.05	Os03g0796800	Similar to guanylate-binding family protein.							1				3				2	3	1			10	**5**
1.65	Os07g0584750	Similar to OSIGBa0147H17.4 protein.					1	1					4				1	-	1	3		11	**6**
1.05	Os04g0655700	Similar to OSIGBa0147J19.14 protein.					1						3				2	3		2		11	**5**
1.53	Os07g0127700	Similar to Pathogenesis-related protein class 1.					1						6					2		2		11	**4**
1.43	Os06g0127800	Dwarf and low-tillering; GAI-RGA-SCR											3	1			1	4		2	1	12	**6**
1.88	Os11g0154900	Similar to DNA-binding factor of bZIP class											5				1	4		2		12	**4**
1.2	Os10g0461100	Similar to Keratin, type II cytoskeletal 1					2						3					3	2	2		12	**5**
1.2	Os01g0884300	No apical meristem											4				1	5		3		13	**4**
1.12	Os08g0408500	Pathogenesis-related transcriptional factor and ERF								1			4				2	4		2		13	**5**
1.1	Os05g0438800	Similar to Actin 1.					1						5				1	4		2		13	**5**
1.08	Os08g0187800	Similar to Glucose-6-phosphate/phosphate-translocator precursor.					3						3					3	2	3		14	**5**
Total of occurences (number of genes)			**1**	**1**	**2**	**2**	**72**	**21**	**8**	**2**	**2**	**6**	**2**	**100**	**16**	**2**	**2**	**141**	**183**	**53**	**201**	**16**		