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Distinct Structural and Functional Characteristics of Stress-Related Genes of Different Plants Revealed by *In-silico* Analysis

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Abstract

Plants always have to fight against various environmental stress conditions like cold, drought, salinity, submergence, etc. The prime target of recent research in plant biology is to unveil the intricate series of events in responses and adaptation to different stress conditions. Sufficient *in-silico* computational studies are yet to be done to distinguish the stress related genes from the non-stress related ones. As common mechanisms of stress responses exist among different plants, we sought to identify the general structural and functional features that may be hidden in stress related genes of different plant species. We assumed that these features in stress-related genes might be different from non stress related genes. One hundred and sixty stress-responsive genes from five different plant species were studied. Computational and bioinformatics studies were done to determine several structural properties like length of gene, exon, intron, UTRs as well as to identify overrepresented sequence motif and enrichment of gene ontology (GO) functions. The UTRs of stress related genes were found to be significantly different from non-stress related signal transduction, cellular components like thylakoid and molecular functions like oxidoreductase activity are significantly enriched for stress related genes. Further studies are required to identify more stress specific features of plant stress genes which may help to establish a computational model for detecting stress related genes from various gene lists.

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Keywords

Plant stress; Bioinformatics; UTRs; Motif; Gene ontology; Enrichment

Introduction

As plant cannot migrate from one place to another, harsh environmental conditions can be an important cause of mortality for plants. Environmental stresses can be biotic caused by different plant pathogens or abiotic such as cold, drought, salinity, submergence, heavy metals, radiation, etc. These stresses have great influence on the evolution of plant species and also have detrimental effects on plant growth and agricultural productivity [1,2]. Nowadays, due to the abiotic stresses the estimated gap between the attainable and actual yields of crops is 40 - 50% [http://www.isaaa.org/]. Thus, introduction of crop varieties with enhanced tolerance to environmental stresses and sustainable growth rate under suboptimal conditions are the crucial objectives in modern agriculture.

Using *Arabidopsis thaliana* and *Oryza sativa* (rice) as model systems, various genes were over expressed in these which led to the identification of stress tolerant genes and transcription factors [3,4]. Many other studies have also been done with the model plant *Arabisopsis thaliana* to elucidate the biochemical pathways of stress perception, signal transduction and adaptive responses [5-8].

Functional basis of stress tolerance should be explained on the basis of molecular mechanism and energetic vacillation. The mechanistic viewpoint of stress tolerance focuses on the similarities between cellular responses to different types of stresses [9]. To perceive environmental stresses and to response to them, plants have evolved the mechanisms of complex signaling crosstalk such as interactive and antagonistic actions of different phytohormones like salicylic acid (SA), jasmonic acid (JA), ethylene (ET), abscisic acid (ABA), etc [10]. They regulate the prophylactic responses against both biotic and abiotic stresses. Again the generation of reactive oxygen species (ROS) has been proposed to be a common response in different stress conditions [10].

Plants produce energetic resources to activate the mechanisms of stress tolerance and survival. These metabolic shifts of energy reallocation represents a common response occurred under different adverse conditions [1,11,12]. Recently it was shown that modulation of cellular energy homeostasis and increased pool of NAD+ and NADH may play role to improve the yield of crop in environmental stress conditions [13,14].

Stress resistance traits that are functionally correlated with different stress mechanisms have been identified by quantitative genetic studies [11,15,16]. The complex mechanisms of stress perception, signal transduction and intonation of gene expression in stress environment have partially been uncovered by functional genomics study [17]. It was found that in transgenic rice (Orvza sativa), stress-responsive transcription factor SNAC1 over expression enhance drought resistance significantly [4]. Stress response mechanisms bring great changes in global gene expression, manner of protein modification and compositions of different metabolites [18]. Recently non-coding RNA has been found to be involved in stress response mechanisms of plants [19]. In last decade, it was revealed that the expression of different but overlapping gene suits are regulated by both biotic and abiotic stresses [20]. Some heat-shock proteins are generally stimulated as a common response to various stress environments [21,22]. Again, DREB transcription factors and phytochrome abscisic acid (ABA) have been identified as shared components in drought, salinity and unusual temperature responsive pathways in Arabidopsis model system [23,24].

The existence of some genes associated with general stress responsive mechanisms has been discovered by extensive study from the viewpoint of the cell physiology [25,26], evolutionary biology [1,12] and most importantly biotechnology [27-29]. The elucidation of the complex biochemical networks and structural properties of these stress responsive genes may provide targets that lead to the production of engineered stress resistant plant species.

Sufficient computational studies have not yet been done to identify significant characteristics of stress responsive genes that can differentiate them from non-stress related genes. Only a few studies were carried out to discover the stress responsive DNA regulatory motifs in Arabidopsis thaliana [30,31]. Due to the insufficient data on general structural properties of plant stress related genes, no computational method could be devised to predict stress related genes. For these reasons, laborious and cumbersome wet lab analyses have to be done to identify even a single stress related gene. In this study bioinformatics and computational analyses were performed with stress and non-stress related genes from five different plant species (Arabidopsis thaliana, Oryza sativa, Zea mays, Solanum lycopersicum and Glycine max) to identify generalized structural properties (gene length, exon length, motifs, length of 5' and 3' untranslated regions) of stress responsive gene that will distinguish them from non-stress related genes. This effort may be helpful to develop tools to identify stress related genes in silico. We have examined the Gene Ontology (GO) annotations in the group of stress related genes of these plant species to delineate the trends in the biology of stress responses.

Materials and Methods

Datasets

List of stress related genes were obtained from Plant Stress Gene Database (http://ccbb.jnu.ac.in/stressgenes/frontpage.html) [32]. A total of 160 stress related gene sequences from five plant species (Arabidopsis thaliana, Glycine max, Oryza sativa, Solanum lycopersicum and Zea mays) (out of available 259 stress related genes from 11 plant species), were used in this study. The gene sequences, both stress and non-stress, were downloaded through the Biomart portal of Ensembl Plants, release - 19 (http://plants.ensembl. org/biomart/martview). The datasets used in this study are Arabidopsis thaliana (TAIR10 GCA 000001735.1 2010-09-TAIR), Glycine max (V1.0 GCA 000004515.1 2012-07-JGI), Oryza sativa (MSU6 GCA 000005425.2 2009-01-MSU), Solanum lycopersicum (SL2.40 GCA 000188115.1 2011-04-ITAG), and Zea mays (AGPv3 2010-01-MaizeSequence). The stress related genes were subtracted from entire genome dataset and the remaining data were used as negative dataset. There are 160 stress related genes (for detail list see supplementary Table S1) are included in positive dataset of which 33 from Arabidopsis thaliana, 55 from Glycine max, 9 from Oryza sativa, 26 from Solanum lycopersicum and 37 from Zea mays; whereas 256672 genes were included in negative dataset, of which 34259 from Arabidopdid thaliana, 56709 from Glycine max, 65518 from Oryza sativa, 34689 from Solanum lycopersicum and 65497 from Zea mays.

Length Analysis

Genomic location information of features like genes, exons and UTRs for both positive and negative dataset was obtained from the Ensembl Plants databases using Biomart portal. Their lengths were calculated using in house Perl script. For statistical significance, 1000 random sets for each feature, consisting of 160 members, were produced from negative dataset. The Z score and p-value of significance were calculated from these datasets using R statistical programming [33,34]. Distribution of both 5' and 3' UTR length are represented in Box-Whisker plot. Significance of difference of UTR length between stress related genes and non-stress related genes was calculated using Wilcoxon test.

Motif Analysis

MEME (Multiple Em for Motif Elicitation) [35,36] package (version 4.9.1) was used to identify the significantly over-represented motif in stress related genes (positive dataset). Thousands of random datasets consisting of 160 gene sequences each were produced from negative dataset and searched for similar motif using the position weight matrix (PWM) of MEME and STORM program [37] specifying the p-value cut off 0.00001. Z-score and p-value of significance were calculated using the random dataset (expected") and the positive dataset ("observed") with R statistical programming [33,34].

Functional Enrichment Analysis

Functional annotation of plant stress-related genes is based on Gene Ontology (GO) (Consortium, 2000; http://www.geneontology.org) [38] extracted from Ensembl Plant (release - 19). Accordingly, all genes are classified into three ontology categories (i) biological process (BP), (ii) cellular component, (CC) and (iii) molecular function (MF) and pathways when possible. We considered only those GO pathway categories that have at least 9 genes annotated. We used Gitools [39] for enrichment analysis using non-stress related genes as background, and for heatmap generation. Resulting p-values were adjusted for multiple testing using the Benjamin and Hochberg's method of False Discovery Rate (FDR).

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Results and Discussion

Results

The length of UTRs of stress related genes differ significantly from non-stress related genes in different plant species

Genes encode proteins which are the key functional components in different cellular mechanisms. Upstream and downstream sequences of genes play role in the regulation of gene expression. We calculated the length of stress related genes, their exons, 5' and 3' UTRs, and compared those to non-stress related genes to determine if any significant difference exists. For gene length and exon length, no statistically significant difference was obtained between stress and non-stress related genes. But z-score and p-value confirmed the significant difference in 5' and 3' UTR lengths when

compared between species. It was further confirmed by Wilcoxon test (Figure 1). In case of 3' UTRs, significant difference was obtained for *Glycine max* and *Solanum lycopersicum* with p-value 1.078e-05 and 3.145e-06, respectively. In case of 5' UTRs significant difference was obtained for *Arabidopsis thaliana*, *Glycine max*, *Oryza sativa* and *Solanum lycopersicum* with p-value of 6.54e-09, 0.0001262, 6.084e-06 and 6.315e-06, respectively. These distinct UTRs of stress related genes may play important role in more stringent regulation of gene expression in stress conditions.



Figure 1: Box-and-whisker plots show distribution of UTR length of stress genes and non-stress genes. Each pair (V1-V2; V3-V4) represents UTR from one plant species. Left side box-plot in each pair shows UTR lengths of stress genes and right side box of that pair represents UTR length of non-stress genes. In this, star mark indicates that the difference of UTR length between stress genes and non-stress genes is significant. (a) Box-plot results of 3' UTRs (b) Box-plot results of 5' UTRs.

Stress related genes contain specific and significantly overrepresented small motif

At this stage we sought to know if there is any common short sequence motif that significantly prevails in stress-related genes. We used MEME package [35,36] to search for overrepresented motifs in 160 stress-related genes. One significantly overrepresented G-C rich motifs was obtained with the e-value 1.1e-007. This motif was selected for further analysis (Figure 2). This is a 12 nucleotides long motif with pattern GGC[GT]GC[TG]GC[GTA]GC. In non-stress related genes the frequency of occurrence of this motif was searched by STORM program [37]. From non-stress related gene dataset 1000 sets, each consisting of randomly selected 160 genes, were constructed to use as control for this purpose. To find the significant difference in the frequency of occurrence of this motif, z-score was calculated. The occurrence of this motif in non-stress related genes was not significant, which implies for its highly specific association with stress related genes.

Important biological processes, cellular components and molecular functions are enriched for stress related genes

Functional enrichment analysis is performed to assign biological meaning to genes. It is performed to assess if a gene or a group of genes show any significant over-representation of any biological characteristics. In this study Gitools [39] was used for enrichment analysis using Gene Ontology (GO) [38] database. GO database centralizes and disseminates the prior knowledge of known gene which allows researchers to assign attributes to their experimentally identified genes. Stress related genes of five plants were analyzed in a background of non-stress related genes, to determine the enrichment of particular biological processes (BP), molecular functions (MF) and cellular components (CC) as termed by GO. Detail statistical results are presented in supplementary tables (S2 to S12). The stress related genes of Arabidopsis thaliana were enriched for removal of superoxide redicals, generation of precursor metabolites and energy, thylakoid, metal ion binding, copper ion binding, chromatin binding, etc (Figure 3 and Table 1). Glycine max stress related genes were enriched for transferase activity, oxidoreductase activity, etc (Figure 4 and Table 2). In Oryza sativa these were enriched for plasma membrane localized proteins (Figure 5 and Table 3). The stress related genes of Solanum lycopersicum were enriched for oxidoreductase activity, organelle, etc (Figure 6 and Table 4). In Zea mays they were enriched for small GTPase mediated signal transduction, oxidation-reduction process, carbohydrate metabolic process, biosynthetic process, plasma membrane, cytoplasm, organelle, chloroplast, GTP binding, oxidoreductase activity, nucleotide binding, etc. (Figure 7 and Table 5). In this analysis oxidoreductase activity was found to be a common mechanism to stress response in almost all plants. Some findings from this analysis are seemed to be specifically significant like thylakoid and chromatin binding of A. thaliana and small GTPase activity of Zea mays. From literature mining enough supporting data regarding the significant association of these components with stress were obtained. In Arabidopsis, ascorbate peroxidase bound to thylakoid contributes in scavenging reactive oxygen species produced in different stress conditions [40]. Arabidopsis TAAC (Thylakoid ATP/ADP Carrier) gene is highly up-regulated in leaves under different stress environments [41]. Gene activation in dehydration stress responses depends on a specific pattern of histone modification and chromatin structure [42]. H3K4me3 (H3 Lys4 trimethylation) has a function as epigenetic marker of stressed memory [43]. Epigenetic regulations mediated by the modification of histone proteins are conserved in plant [44]. Modifications on the sites of H3K4 and H3K9 are correlated with the activities of abiotic stress responsive genes in Arabisopsis [45]. In Arabidopsis, Rop GTPase signalling influences the mechanisms of alcohol dehydrogenase activity at low O2 condition [46]. Monomeric RopGTPases regulate the production of H2O2, responses to hormones, programmed cell death, etc [47]. As small GTPase activity was significantly enriched in Zea mays, it can

be deciphered that they may play similar role in this plant as in Arabidopsis. From this enrichment analysis, it can be concluded that components enriched in different plants are highly co-related with different stress conditions and can be considered as distinct features of plant stress related genes.



Figure 2: Selected motif obtained from MEME analysis. This is represented by position-specific probability matrices that specify the probability of each possible letter appearing at each possible position in an occurrence of the motif. There are stacks of letters at each position in the motif. The total height of the stack is the "information content" of that position in the motif in bits. The height of the individual letters in a stack is the probability of the letter at that position multiplied by the total information content of the stack.



GO term for Biological Process	Total studied	Observed	Expected mean	Corrected
	Gene			right-p-value
Removal of superoxide redicals	33	7	0.0117853635	5.81E-16
Response to cadmium ion	33	8	0.4586470641	3.66E-6
Generation of precursor metabolites and energy	33	6	0.5823933811	0.0015
Response to auxin stimulus	33	5	0.3594535877	0.0015
Oxidation reduction process	33	8	1.3287997381	0.0023
Positive regulation of transcription, DNA dependent	33	5	0.4537364959	0.0033
Regulation of transcription, DNA dependent	33	9	1.8404809381	0.0035
Carbohydrate metabolic process	33	8	1.909228892	0.0157
Secondary metabolic process	33	5	0.7081039255	0.0155
GO term for Cellular Component				
Thylakoid	33	6	0.4910568137	0.0019
GO term for Molecular Function				
Metal ion binding	33	7	0.2632064522	4.77E-6
Copper ion binding	33	5	0.2386536115	6.31E-4
Chromatin binding	33	5	0.3280259516	0.0021
DNA binding	33	10	2.0182435047	0.0036
Sequence specific DNA binding transcription factor	33	8	1.6509330079	0.0168
Nucleic acid binding transcription factor activity	33	8	1.6519151216	0.0147
Oxidoreductase activity	33	8	1.6764679623	0.0144

Table 1: Enriched Gene Ontology terms for stress related genes of Arabidopsis thaliana

P-value

Enriched GO term



transferase activity, transferring alkyl or aryl (other than methyl) groups oxidoreductase activity ion binding

Glycine max

Figure 4: Significantly enriched GO terms for the stress related genes of Glycine max. The red color coding indicates the significance of the p-value as described in Figure 3.

GO term	Total	Observed	expected-mean	Corrected right-p-value	
	Studied				
	Genes				
Transferase activity, transferring alkyl or aryl (other than methyl) groups	55	22	0.12182966	9.28E-41	
Oxidoreductase activity	55	15	2.9300033226	1.89E-5	
Ion binding	55	14	5.437663824	0.025	

Table 2: Enriched Gene Ontology terms for stress related genes of Glycine max

P-value	Enriched GO term
	plasma membrane
	Oryza sativa
Figure 5: Significantly enriched The red color coding indicates the	GO terms for the stress related genes of Oryza sativa. as significance of the p-value as described in Figure 3.

GO term	Total Studied genes	Observed	Expected-mean	Corrected right-p-value
Plasma membrane	10	4	0.3035335430	0.0385



GO term	Total	Observed	Expected-mean	Corrected
	Studied			right-p-value
	Genes			
Oxidoreductase activity	26	8	1.2154928765	0.0021359861
Organelle	26	8	1.2589836765	0.0018170424
Cytoplasm	26	6	0.9020591798	0.0061442772
Intracellular	26	9	2.1580434908	0.0062167642
Ion binding	26	7	2.0980561804	0.0478418769

Table 4: Enriched Gene Ontology terms for stress related genes of Solanum lycopersicum



lecular Function. The red color coding indicates the significance of the p-value as described in Figure 3.

GO term for Biological Process	Total Observed	Observed	Expected-mean	Corrected
	Genes			right-p-value
Small GTPase mediated signal transduction	41	8	0.0506382897	8.78E-14
Signal transduction	41	9	0.2282392476	2.19E-10
Oxidation – reduction process	41	9	0.6502249947	8.91E-7
Carbohydrate metabolic process	41	7	0.4109774233	4.93E-6
Biosynthetic process	41	10	1.2270611638	9.41E-6
GO term for Cellular Component			·	
Intracellular	41	22	2.8695030804	3.05E-11
Membrane	41	13	0.9826763746	1.15E-9
Cytoplasm	41	16	1.8493984048	2.85E-9
Plasma membrane	41	10	0.5753683926	9.67E-9
Organelle	41	13	2.3095463412	1.04E-5
Chloroplast	41	7	0.5438111976	1.59E-5
Plastid	41	7	0.6186677997	3.36E-5
GO term for Molecular Function			·	·
GTP binding	41	8	0.1343015508	4.51E-10
Oxidoreductase activity	41	9	0.7192104907	5.41E-6
Nucleotide binding	41	9	0.7705826686	7.23E-6
Metal ion binding	41	7	0.5739006161	6.78E-5
Ion binding	41	8	1.3518221673	0.0016

Table 5: Enriched Gene Ontology terms for stress related genes of Zea mays

Discussion

Environmental stresses are limiting factors for plant growth. Extensive studies are being done on Arabidopsis and some other plants regarding their responses to different environmental stresses. But not enough data are available on mechanisms of stress responses in most of the plants. Even all the stress responsive genes are not identified yet and the mechanisms of stress responses are not completely known. Some bioinformatics studies have been done to identify specific features of regulatory regions of stress related genes [30,31] but not in the region of genes themselves. In this study bioinformatics and computational analyses were performed with plant stress related genes listed from plant stress gene database [32].

Each gene is flanked by short 5' and 3' untranslated regions (UTRs) followed by gene start site and gene end site [48]. Computational analyses identified significant differences in the length of 5' and 3' UTRs between stress related and non-stress related genes (Figure 1). The significant differences calculated as z-score and p-value by Perl scripts, were further confirmed by the Wilcoxon test. It is well established that the regulation of gene expression become highly stringent in different stress conditions [49-52]. UTRs play vital roles in the regulation of gene expression [53-59]. Therefore, distinct UTRs of stress related genes may play pivotal roles to ensure tight regulation of gene expression in stress environments. Further analysis should be propounded to discover the exact role of distinct UTRs in stress conditions.

Distinct motifs were discovered in the regulatory regions of plant stress related genes in previous studies [30,31]. But in this study, by MEME analysis with the clause that the motif should exist in 50% or more genes, a small G-C rich motif (Figure 2) was obtained in the regions of genes. The p-value justified that the motif was significantly overrepresented in stress related genes. The frequency of occurrence of these motifs in non-stress related genes calculated by STORM program with PWM was accountably low. This result corroborates the possibility of occurrence of such distinct motifs in stress related genes. Occurrence of such motif insinuates that it may have important role in up-regulation, down-regulation or epigenetic regulation of genes in stress condition. Further extensive studies including more plant species and newly discovered genes are necessary to discover more such motifs and their plausible roles.

In past decade, each gene product was studied individually to assign its role in biological process but now tools exist to make this process automated. Gitools is such a tool used in this study. Primarily a group of genes are clustered based on some common properties. Enrichment analysis is performed to assess if a group of genes shows any significant over-representation of any biological characteristics. In this study, after detecting the over-represented biological characteristics of stress related genes, data mining was performed manually to explain their possible role in stress responsive mechanisms of plants.

Oxidative stress in plants is a common scenario in different stress conditions like cold, submergence, drought, salinity etc. [60-64]. In our enrichment analysis oxidoreductase activity was significantly enriched in stress related genes of almost all plants included in the study (Figure 3, 4, 6, 7 & Table 1, 2, 4, 5), which is coherent with this scenario. Therefore oxidoreductase activity can be considered as a specific feature of plant stress related genes.

Small GTPase mediated signal transduction was significantly enriched in Zea mays. The G proteins have important role in signal transduction. They mediate the signal transduction to downstream effectors [65]. In rice, a small GTPase, Rac1, regulate the death of hypersensitive cells in innate immune response while heterotrimeric G protein regulates the Rac1 [66,67]. Low O2 regulates the ADH (alcohol dehydrogrnase) activity that depends on RopGTPase signaling in Arabidopsis [68]. Chromatin binding was significantly enriched as molecular function in Arabidopsis thaliana which insinuates toward the epigenetic correlation with stress conditions. Though it is not well understood whether chromatin mediated regulation has positive effects on stress tolerance, it is obvious that there are correlations between epigenetic modifications and plant stress responses [43]. It was observed that linker histones and HMGB (High Mobility Group) proteins play role in abiotic stress responses [69]. Promoter specific histone modification H3K4me3 plays an important role in dehydration and ABA stress responses [70]. In drought response, some lysine modification states on histone H3 N tail are altered which revealed that upon gene activation in stress responses histone modification states changes [42]. From these data it can lucidly be told that small GTPase mediated signal transduction and chromatin binding are the specific phenomena in different stress conditions.

Again, in Arabidopsis, only the cellular component, thylakoid was enriched. This result indicates toward the unique role of thylakoid in stress responses. It has been discovered that stresses have significant effects on the different components of thylakoid [40]. The transcript level of OsCYP20-2 gene in thylakoid lumen of rice is highly regulated under abiotic stress conditions and CYP20-2 gene is also found to be well conserved in some photosynthetic plants [71]. TLP18.3 gene is up regulated in dehydration stress and thylakoid protease Deg2 consorts in stress related degradation of Lhc6, light harvesting protein of photosystem II, in Arabisopsis thaliana [72,73]. Therefore, thylakoid is a very important cellular component that may have more crucial role in stress responses than other organelles in Arabidopsis. Some other molecular functions, biological processes and cellular components (shown in Figure 3 - 7 and Table 1-5) were significantly enriched in stress related genes. All these findings from enrichment analysis can be considered as significant and specific features of stress related genes.

Conclusions

In this study, structural and functional analyses have been done with plant stress related genes with a view to identify hidden features that can discriminate them from non-stress related genes. Extensive computational and bioinformatics analysis were performed and differential outcomes gave an overall idea that discriminating features between stress related and non-stress related genes exist at every level of biological hierarchy. The different UTRs length, existence of distinct G-C rich motifs and selectively enriched some biological phenomena and constituents like small GTPase mediated signal transduction, chromatin binding, oxidoreductase activity and thylakoid identified as stress specific features prove this decipherment.

This analysis proved that there are specific features hidden in stress related genes which are different from non -stress related genes. It can be suggested that further studies should be done by including updated and classified data of plant stress to identify more common and specific features. If enough features can be identified which are highly specific for stress related genes and also discriminating from non-stress related genes, a computational model can be devised that can discern stress related genes from the stockpile of genes.

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