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In Silico Prediction and Functional Characterization of Genes Related to Abiotic and Biotic Stresses in Chickpea (*Cicer arietinum*)

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Abstract: Chickpea (*Cicer arietinum* L.) is second largest grown legumes worldwide contributing 75% of total pulse production. It is a cool season legume crop and grown in tropical and subtropical areas. Due to drastic climatic changes, chickpea suffers from many biotic (blight and wilt) and abiotic (salinity, drought, cold) stresses that directly impact the growth and yield. In our study, we predicted and annotated the genes related to biotic and abiotic stresses. Total 20162 ESTs for salinity, 34346 for drought and 191 for cold stress were downloaded. For biotic stresses, *viz*., wilt and blight disease, 7866 and 56 ESTs were collected, respectively from public domain. All these ESTs were assembled into contigs and blast against protein non-redundant database. Each blast results were mapped to get the corresponding GO terms. Total 1631, 3133 and 13 contigs for salinity, drought and cold stress showed 1333, 2693 and 7 GO terms respectively, while 1144 contigs for *Fusarium* wilt and 6 contigs for *Ascochyta* blight disease showed 955 and 4 GO terms. These GO terms describe biological process, molecular function and cellular components of corresponding stresses. Remaining 298 (salinity), 440 (drought), 6 (cold), 189 (wilt) and 2 (blight) contigs were mapped to reference genome and further used for annotation using gene prediction methods and promoter analysis. This study provide insight to novel gene related to abiotic and biotic stress mechanism that can be further analyzed in molecular biology studies for breeding programs.

Keywords: Abiotic, Annotation, Biotic Stress, Chickpea, Gene Prediction

Introduction

Chickpea, a member of *Fabaceae* family also known as legume family is of varied nutritional and economic values. Studies show that chickpea seed comprise of 3-6% oil content, 40% carbohydrate and 20-30% crude protein (Jha *et al*., 2014). The climate requirement of chickpea is very favorable as it can easily grow in tropical and sub-tropical regions during winters that make it third highest produced legume crop in world and highest in Asia (Gaur *et al*., 2010). India is the largest producer of chickpea, comprising of 68% of global production as compared to America (3.8%), Africa (4.8%) and Europe (0.9%). Total production of 13.1 million tons from an area of 13.5 million ha and a productivity of 9676 Hg/ha was recorded in year 2013 (FAOSTAT, 2012).

Comparative statistics of the global versus Indian chickpea production, area harvested and yield shows that India has major impact and contribution on global chickpea requirement. Various unfavorable conditions during life cycle of chickpea, especially during growing season causes approximately 50% yield loss each year and are increasing every year (Krishnamurthy *et al*., 2010; Ahmad *et al*., 2005; Varshney *et al*., 2010). Among the abiotic stresses, drought and salt stress are the major reasons for loss in production. Reports depicted 6.4 million tons yield loss due to abiotic stresses, out of

which more than 40% occurred from terminal drought (Garg *et al*., 2016). Abiotic stress (drought, cold and salinity) contributes economic loss of approximately1.3 billion, 186 million and 354 million US dollars, respectively (Ryan, 1997). Among the various abiotic stresses affecting chickpea production, drought stress, particularly at the end of the growing season is a major constraint to chickpea production and yield stability in arid and semi-arid regions of the world. World's 20% of cultivable land is unable to provide quality yield due to increased soil salinity and high salt concentrated water used for irrigation (Flowers *et al*., 2010; Selvakumar *et al*., 2014). Other than abiotic stress, various biotic stresses also affect yield loss of 4.8 million tons (Ryan 1997). Supplementary Table S1 shows many biotic diseases listed in literature with their causative age.

Many fungal diseases damage this crop, of which Ascochyta blight disease caused by *Ascochyta rabiei* is very important, leading to severe damage. Sometimes, it results into complete yield loss due to blight formation during flowering and podding stage (Nene, 1982; Nene *et al*., 1996). *Fusarium oxysporum* pathogen infected seedlings show leaf drop and collapse due to browning and blackening of xylem (Kraft *et al*., 1994) causing wilt disease. Another rust causing fungus, *Uromyces ciceris-arietini* infects the plant seedlings with visible round, brown spots causing leaf drop to death of plant (Stuteville *et al*., 2010). Phytoplasma are specialized bacteria that causes phyllody (Pallavi *et al*., 2012). Due to adverse climate and pathogen scenario, there is a great necessity to develop varieties resistant to such biotic and abiotic stresses.After the draft genome of chickpea, which was sequenced in 2013 (Varshney *et al*., 2013; Jain *et al*., 2013) ways to explore the novel and unpredicted stress genes expressing in biotic and abiotic stresses has been created.

There is a gap between potential and produced yield due to these stresses and need to fill by regulating corresponding genes. Although there are few studies available for identification of abiotic/biotic stress responsive genes using allele diversity approach (Roorkiwal *et al*., 2014) and microarray analysis (Mantri *et al*., 2007), but there are many unexplored genes that control stress responses and triggered stress responsive pathway by regulating corresponding transcription factors (Chen and Zhu, 2004). Available information and techniques for chickpea crop improvement needs more candidate genes for breeding strategies *viz*., gene pyramiding, marker assisted recurrent selection, multiline strategy.

In our study, efforts are made to understand the biology behind the stress conditions and characterization of genes that are getting expressed. In addition to functional characterization, computational analysis has been done to predict the novel candidate genes and their mapping on chromosome which can provide a good insight into complex abiotic/biotic stress tolerance pathways.

Materials and Methods

ESTs sequences related to abiotic and biotic stresses in chickpea were downloaded from NCBI-EST (http://www.ncbi.nlm.nih.gov/). Boolean search has been performed with the keywords like chickpea with salinity, drought, cold, fusarium wilt, Ascochyta blight and Chickpea rust. Figure 1 describes the flow of analysis for gene prediction and functional characterization. These ESTs were aligned and merged to reconstruct the gene sequences. Pre-processing of these ESTs were performed for repeat masking and cleaning, which was followed by assembly using EGassembler (Masoudi-Nejad *et al*., 2006). The generated contigs from EGassembler were considered for further analysis.

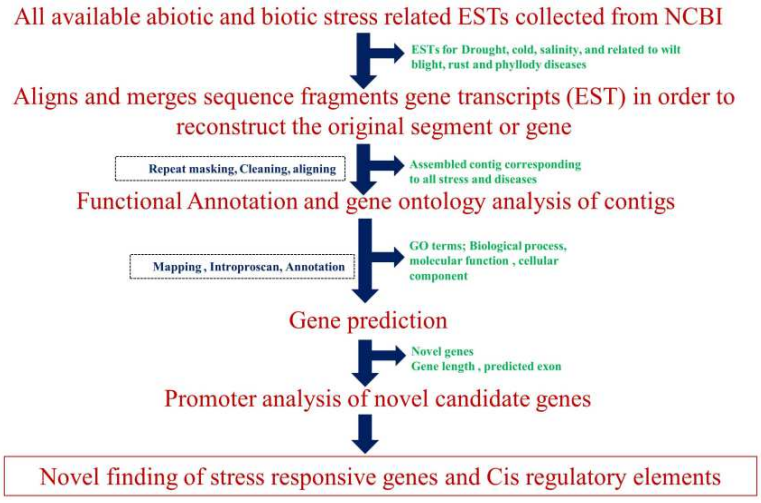

Fig. 1: Analysis work flow for gene prediction and functional characterization

Functional Characterization and Annotation

Contigs assembled by EGassembler were annotated using Blast2GO Pro (Conesa *et al*., 2005) pipeline. Blastx (Altschul *et al*., 1990*)* was used to annotate the contigs for each stress individually. This was followed by mapping and InterProscan (Quevillon *et al*., 2005) to retrieve complete information of Gene Ontology (GO) and domains of annotated contigs searched against protein database for all six reading frames. Each GO term describes its involvement in molecular function, biological process and cellular component. Unannotated or uncharacterized contigs from all stress datasets were filtered out for gene prediction.

Identification and Prediction of Unannotated Contig

Filtered unannotated contigs were stored in fasta file format and subjected to *ab initio* gene prediction tool, FGENESH (Salamov and Solovyev, 1998) accessed through MolQuest version 2.4.5.1135 (http://www.molquest.com) for prediction of genes.

Linkage Map and Promoter Analysis

Predicted candidate genes were located on chromosomes and a linkage map has been created for disease/ stress findings using chickpea genomic web resource (http://www.nipgr.res.in/CGWR/home.php) (Kumari *et al*., 2014). All the predicted genes were searched in PLACE (Higo *et al*., 1999) database for identification of *cis*-elements, motifs, corresponding transcription factors and its description in other species.

Results and Discussion

In this study, chickpea ESTs related to abiotic stresses, like salinity, draught and cold downloaded were 20162, 34346 and 191, respectively. Among the biotic stresses in chickpea, wilt, blight, rust and phyllody diseases ESTs obtained were 7866, 56, 2 and 3 ESTs, respectively. A total of 1631, 3133 and 13 contigs were generated by EGassembler for salt, drought and cold stress, respectively. Similarly, 1144, 6, 1 and 1 for contigs were generated for wilt, blight, rust and phyllody, stress, respectively (Table 1).

Functional Annotation and Prediction of Candidate Genes

Blast2Go Pro annotated total 1333, 2693 and 7 contigs related to salinity, drought and cold stress, respectively. Annotation was not obtained for contigs from rust and phyllody ESTs, while 955 and 4 annotation were recorded for wilt and blight related contigs, respectively. All these annotation were mapped to different GO categories *i.e.,* biological process, molecular function and cellular components. Distribution of GO terms showed that 45%-47% were related to biological process, 33-36% to molecular functions and 19-20% to cellular components for drought, salinity, blight and wilt related contigs, respectively (Fig. 2).

Out of these, few contigs remained uncharacterized and did not map to any annotation. Selected uncharacterized contigs listed in Table 1 were subjected to gene prediction using FGENESH. Total 79 genes (salinity), 145 genes (drought), 27 (wilt) and 1 gene (blight) were predicted while, there is no gene was predicted for cold stress, rust and phyllody disease.

Mapping of Candidate Genes and Identification of Cis-Regulatory Elements

All predicted candidate genes were mapped to chromosomes. Mapping of genes shows that all genes were distributed randomly over all 8 chromosomes while many are still unallocated and placed on *UN* chromosome. Major genes lie on chromosome 3, 5 for drought and salinity, while wilt genes are almost equally distributed on all chromosomes. Single gene predicted for blight disease is located on chromosome 4 (Fig. 3-6).

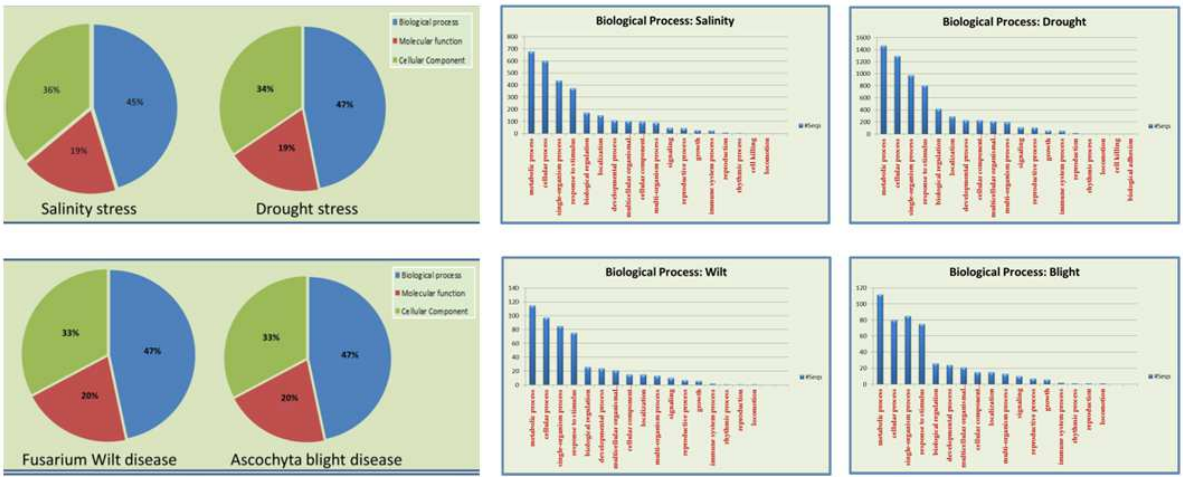

Fig. 2: Distribution of GO terms in abiotic and biotic stress related contigs and sequence distribution in biological process

Table 1: Statistics of overall analysis of stress/disease related ESTs

Abiotic Stress

Stress	ESTs/Nucleotide collected	Contigs generated	GO terms	Uncharacterized	Novel gene finding
Cold	191	13	7	6	0
Salinity	20162	1631	1333	298	79
Drought	34346	3133	2693	440	145

Biotic Stress

Disease	Pathogen	ESTs/ Nucleotide collected	Contigs generated	GO terms	Uncharacterized	Novel gene finding
Fusarium Wilt	*Fusarium oxysporium*	7866	1144	955	189	27
Ascochyta blight	*Ascochyta rabiei*	56	6	4	2	1
Chickpea Rust	*Uromyces ciceris-arietini*	2	1	0	1	0
Phyllody	*Phytoplasma*	3	1	0	1	0

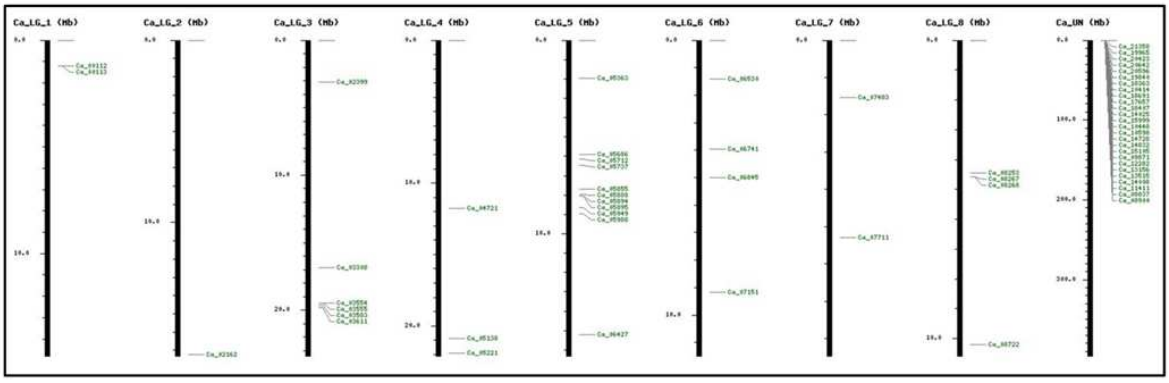

Fig. 3: Chromosomal mapping of drought related predicted genes

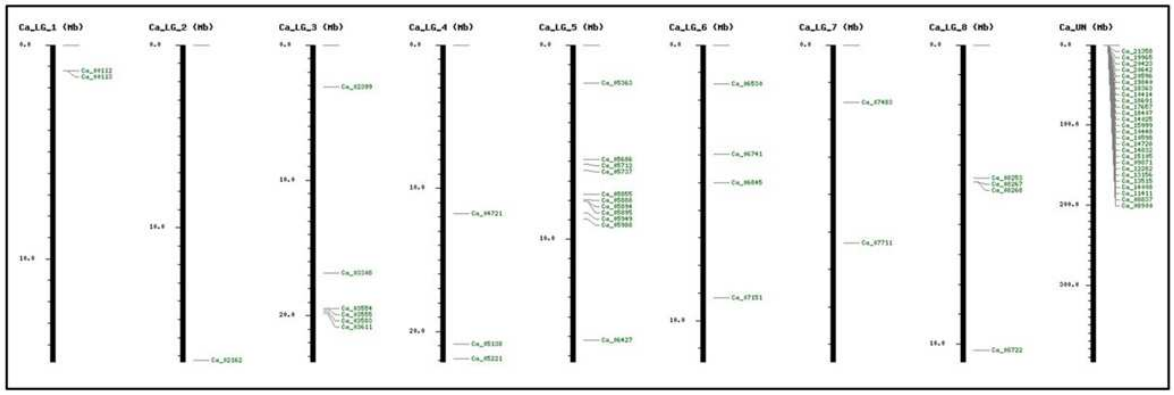

Fig. 4: Chromosomal mapping of salinity related predicted genes

Total candidate genes located on chromosome shows that 39 genes are activated during exposure of both stresses while 20 genes are unique for salinity stress and 80 genes for drought stress (Fig. 7). It shows that these can be defense genes and playing major role in stress pathways (Supplementary Table S2).

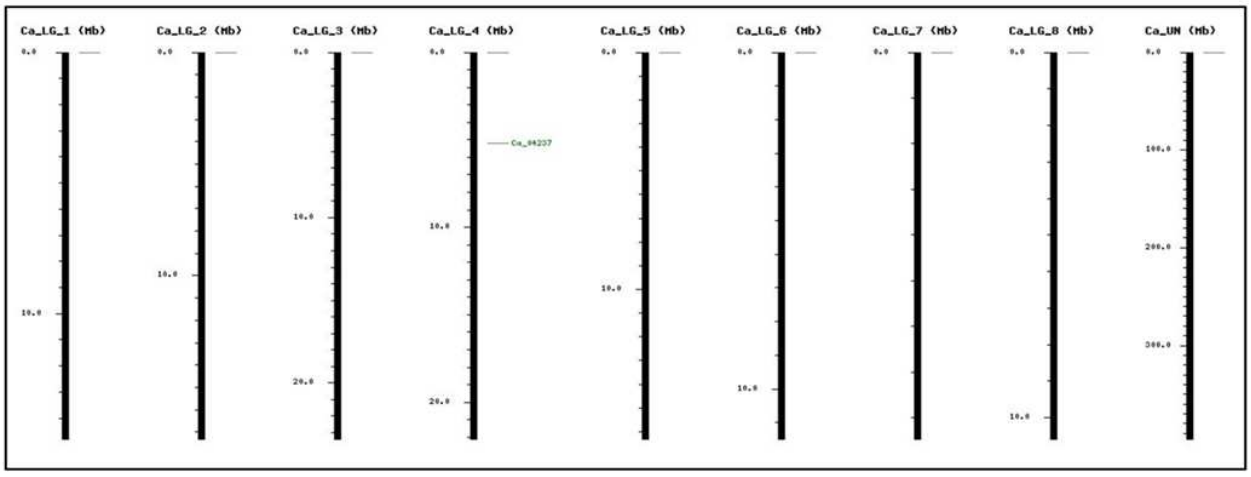

Fig. 5: Chromosomal mapping of Blight disease related predicted genes

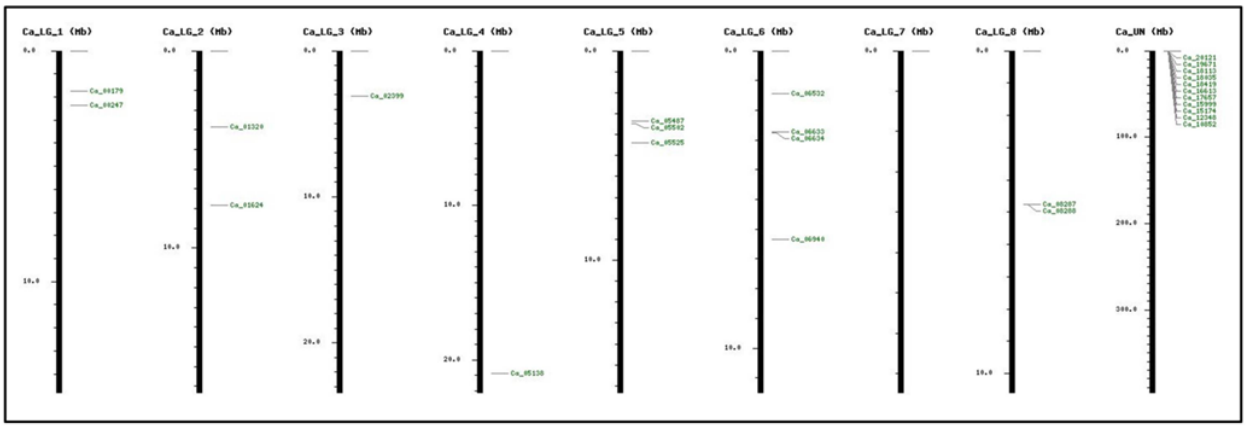

Fig. 6: Chromosomal mapping of Wilt disease related predicted genes

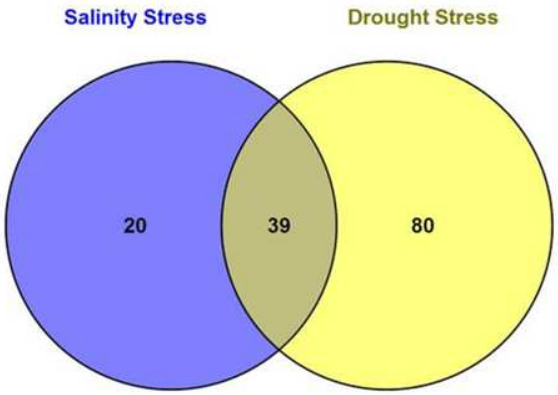

Fig. 7: Venn diagram depicting statistics of crosstalk genes of salinity and drought

Study also includes identification of *cis*-regulatory DNA elements that regulate the biological process in stress or disease conditions. To analyze this, we used PLACE database with all predicted genes as query and identified *cis*-regulatory motifs. Analysis of *cis*-regulatory elements describes the candidate gene expression and corresponding functional transcription factor. It can be suggested that genes which share common regulatory motifs are co-expressing and functioning in biological process in response to the corresponding biotic/abiotic stress. *Cis*-regulatory motifs and functioning transcription factor for each predicted candidate gene shows that in stress, transcription factors like DOF, bZIP, WRKY, RAV, ABRE and MYB are expressed majorly. These transcription factors are also reported in other crops *viz*., DOF in Chinese cabbage (Ma *et al*., 2015), bZIP in tepary bean (*Phaseolus acutifolius*) and common bean (*P. vulgaris*) (Rodriguez-Uribe and O'Connell, 2006) and other five legume genomes (Wang *et al*., 2015), ABRE and WRKY in soya bean (Li *et al*., 2005; Zhou *et al*., 2008).

DOF, which is plant specific transcription factor and known as DNA binding with one finger, contains

conserved C2-C2 zinc finger and plays a significant role in plant growth and transcriptional regulation during stress conditions by aid of mobile proteins (Le Hir and Bellini, 2013; Yanagisawa, 2004). ABRE transcription factor participates in drought and high salinity tolerance in various crops by ABA signaling (Hossain *et al*., 2010). ABRE-binding bZIP transcription factor shows its presence in biotic stress. bZIPis reported as defense transcription factor that works during pathogen attacks in various crops like maize, *Arabidopsis*, rice and cotton and can assume same functioning in chickpea crop for stress management (Alves *et al*., 2013). WRKY transcription factor often functions in many stress responses simultaneously and participate in common signaling pathways. This property of WRKY makes it a good candidate for stress tolerance mechanism (Chen *et al*., 2012). Many predicted genes that were expressed during stress condition contain *cis* elements that provide binding sites to RAV which is known as Related to ABA-insensitiveViviparaous1. RAV transcription factor found to controls drought and salinity responses by participating in ABA independent stress pathway (Fu *et al*., 2014). Similarly MYB Family transcription factor plays role in various biological processes for ABA associated biotic and abiotic stress responses. It regulates functional genes to regulate functions as Phenylpropanoid metabolism, hormone responses, formation of cyclin -type B during plant defense reactions (Ambawat *et al*., 2013). Contig wise transcription factor abundance are listed in Supplementary Table S3.

The candidate genes of stress responsiveness can lead to crop improvement strategies *viz*., transgenic development, linked SNPs identification (Schena *et al*., 1995; Kudapa *et al*., 2013). These genes have been involved in abiotic/biotic stress tolerance in other crops like rice (Abbani *et al*., 2003), *Arabidopsis* (Kreps *et al*., 2002; Seki *et al*., 2002) whose information can be useful for chickpea also. These candidate genes can be selected for corresponding trait of interest on the basis of biochemical pathways and mutational analysis (Zhu *et al*., 2008).

Conclusion

Chickpea is economically very important crop and suffers from various biotic and abiotic stresses during its life cycle. In the present study, genomics approach is applied to predict genes related to drought, salinity, cold and disease caused by pathogen infections from ESTs available in public domain. In this study 1333, 2693 and 7 genes related to salinity, drought and cold stress respectively, were predicted, while 955 and 4 annotations were found for genes related to wilt and blight, respectively. These genes were found to be functional for DOF, bZIP, WRKY, RAV, ABRE and MYB transcription factors. The reported genes can be further used for candidate gene discovery required for Marker Assisted Selection (MAS) or gene pyramiding in crop improvement programme. *Cis*-regulatory elements and transcription factors study provides insight of their role in corresponding stress condition, whose validation is further warranted in Endeavour of improving chickpea productivity.

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Author's Contributions

Sukhdeep Kaur, Satendra Singh and Anil Rai: Conceived this study.

Sukhdeep Kaur and Gitanjali Tandon: Participated in sample collection and data generation.

Sukhdeep Kaur, Mir Asif Iquebal and Sarika Jaiswal: Created the work-flow.

Sukhdeep Kaur: Performed data analysis.

Satendra Singh, **Mir Asif Iquebal, Sarika Jaiswal and Kumar:** Drafted the manuscript. All authors read and approved the manuscript.

Conflict of Interests

The authors declare that they have no competing interests.

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Supplementary Files

Supplementary Table S1. List of various diseases of chickpea collected from literature

Bacterial diseases

Bacterial blight	Xanthomonascampestrispv. Cassia
Bacterial leaf spot	*Burkholderiaandropogonis*
Fungal diseases	
Acrophialophora wilt	*Acrophialophorafusispora*
Alternaria blight	*Alternariaalternata; Alternariatenuissima*
Aphanomyces root rot	*Aphanomyceseuteiches*
Ascochyta blight	*Ascochytarabiei*
Black root rot	Fusariumsolani
Black streak root rot	Thielaviopsisbasicola
Botrytis gray mold	Botrytis cinerea
Collar rot	Sclerotiumrolfsii
Colletotrichum blight	Colletotrichumcapsici; Colletotrichumdematium
Cylindrocladium root rot	Cylindrocladiumclavatum
Damping-off	Pythiumdebaryanum; Pythiumirregulare; Pythiumultimum
Downy mildew	Peronospora sp.
Dry root rot	Rhizoctoniabataticola
Foot rot	Operculellapadwickii
Fusarium root rot	Fusariumacuminatum; Fusariumarthrosporioides; Fusarium avenaceum; Fusariumequiseti; Fusariumsolanif.sp. eumartii
Fusarium wilt	Fusariumoxysporumf.sp. ciceris
Myrothecium leaf spot	Myrotheciumroridum
Mystrosporium leaf spot	Mystrosporium sp.
Neocosmospora root rot	Neocosmosporavasinfecta
Ozonium collar rot	Ozoniumtexanum var. parasiticum
Phoma blight	Phomamedicaginis
Phytophthora root rot	Phytophthoracitrophthora; Phytophthoracryptogea
Phytophthoradrechsleri;	Phytophthoramegasperma
Pleospora leaf spot	Pleosporaherbarum; Stemphyliumherbarum
Powdery mildew	Leveillulataurica; Oidiopsistaurica
Rust	Uromycesciceris-arietini; Uromycesstriatus
Sclerotinia stem rot	Sclerotiniasclerotiorum; Sclerotiniatrifoliorum
Scopulariopsis leaf spot	Scopulariopsisbrevicaulis
Seedling or seed rot	Aspergillusflavus; Trichotheciumroseum
Stemphylium blight	Stemphyliumsarciniforme
Trichoderma foot rot	Trichodermaharzianum
Verticillium wilt	Verticilliumalbo-atrum; Verticilliumdahliae
Wet root rot	Rhizoctoniasolani
Viral diseases	
Bushy stunt	Chickpea bushy stunt virus
Distortion mosaic	Chickpea distortion mosaic virus
Filiform	Chickpea filiform virus
Mosaic	Alfalfa mosaic virus
Narrow leaf	Bean yellow mosaic virus
Necrosis	Lettuce necrotic yellows virus; Pea streak virus
Proliferation	Cucumber mosaic virus
Stunt	Bean leaf roll virus
Yellowing	Pea enation mosaic virus
Phytoplasmal diseases	
Phyllody	Phytoplasma

Supplementary Table S2. Sequence information of novel predicted gene

Wilt related genes

>Contig142
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ACCATCAAGAAACTCACTTTCGTCGAGGGTGGACAAACCTTGTATGTGTTGCACAGAATAGAAGCAATTGATGAAGCAAATTTGGGA
TATAATTACAGCATAGTTGGGGGTGCAGGATTGTCAGAGACAGTGGAAAAGATATCATTTGAGGCAAAATTGTGTGAAGGCCCAAAT
GGAGGGTCCATTGGGAAGGTGAGCGTAAAATATCAAACCAAAGGAGATGCTAAGCCCAATGAGAAGGAGGTTCAAGAAGGAAAGGC
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>Contig224
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Supplementary Table S2. Continue:

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Supplementary Table S2. Continue:

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>Contig691

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>Contig704

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A

Blight related Genes

>Contig1

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Salinity related genes

>Contig42

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Drought related genes

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Supplementary Table S3. Contig wise transcription factors for biotic stresses (wilt, blight) and abiotic stresses (salinity and drought)

Wilt Disease

Contig	**Transcription Factor**
Contig142	BELL homeodomain(2), DOF(8), MYB(1), MYB (8), MYC (8), RAV (3), SEBF(1), WRKY (2)
Contig224	BELL homeodomain(1), bZIP (1), DOF(7), ERF (1), G1like(1), MYB (7), NPR(1), RAV(4), SEBF(1), WRKY (2)
Contig246	ASF 1(1), BELL homeodomain(1), DOF(8), ERF (3), MYB(2), MYB (3), MYC(2), RAV (2), W Box(3), WRKY (5)
Contig250	ABRE(2), ASF 1(1), DOF(2), G1like(1), MYB (1), NPR (1), WRKY (1)
Contig283	ASF 1(1), DOF(1), ERF (4), MYB (3), MYC(8), NPR (1), WRKY (5)
Contig357	bZIP (2), DOF(6), G1like(1), MYB (1), MYC(6), RAV (4)
Contig364	ABRE(1), BELL homeodomain(3), DOF(6), MYB (5), MYC(4), SR1 (2), WRKY(3)
Contig442	AGC-box (1), ASF 1(1), bZIP (1), DOF(2), ERF (3), GCC-box(1), MYB(1),MYB (2), MYC(2), NPR (2), RAV (3), WRKY(4)
Contig444	RAV (1)
Contig444b	DOF(1), ERF (1), MYB (3), MYC(4), W Box(1), WRKY (1)
Contig533	ASF 1(2), DOF(3), ERF (1), G1like(1), MYB (1), MYC(4), NPR (2), WRKY (3)
Contig587	DOF(3), G1like(1), MYC(2), RAV (1)
Contig609	ABRE(2), DOF(4), MYC(2), No found(2)
Contig663	ABRE (1), ASF 1(1), BELL homeodomain(2), DOF(3), ERF (1), MYB (2),MYC(4), NPR (2), RAV (1), SR1 (2), WRKY (4)
Contig667	MYC(2), RAV (1)
Contig677	ASF 1(3), bZIP(2), bZIP (1), DOF(1), GCC-box(1), MYB (3), MYC(6), RAV (1),SR1 (2), WRKY (3)
Contig691	DOF(4), ERF (1), GCC-box(1), MYB(2), MYB (8), NPR (1), RAV (1), WRKY (1)
Contig704	ASF 1(1), BELL homeodomain(1), DOF(5), MYC(2), NPR (1), seed specific expression and abscisic acid (ABA) pathway(2), WRKY (2)
Contig728	BELL homeodomain(1), DOF(10), G1like(1), MYB (2), NPR (1), RAV (1), WRKY (1)
Contig730	BELL homeodomain(1), bZIP (2), DOF(9), ERF (1), G1like(1), MYB (7), RAV (1), WRKY (2)
Contig820	BELL homeodomain(2), bZIP (2), DOF(5), MYB(2), MYB (3), MYC(4), NPR(1), RAV (6), WRKY (2)
Contig868	ABRE (1), ASF1(1), DOF(3), ERF (1), GT1like (1), MYB (2), MYC (4), WBox(1), WRKY (2)
Contig953	ASF1(1), bZIP (1), DOF(4), RAV (4), WRKY (1)
Contig1082	BELL homeodomain(2), bZIP (1), DOF(6)
Contig1112	AGC box (1), bZIP (1), DOF(6), GCC-box(2), MYB (4), RAV (3)

Blight Disease

Contig	**Transcription Factor**
Contig1	BELL homeodomain (2), DOF(4), ERF(3), MYB(5),RAV(2), W BOX(1), WRKY(5)

Salinity Stress

Contig	**Transcription Factor**
Contig42	DOF(5), MYB(1), MYB (10), MYC(12), RAV (2)
Contig55	ABRE(1), ASF 1(3), bZIP (1), DOF(4), ERD1 (4), MYB(6), MYB (10), MYC(8),RAV (5)
Contig71	bZIP (1), DOF(4), MYB(1), MYB (2), RAV (3)
Contig125	ABRE(10), AGC-box(1), bZIP (1), ERD1 (6), MYB(1), MYB (2), MYC(6), RAV (2)
Contig139	MYC(2), RAV (1)
Contig165	DOF(5)
Contig167	DOF(1), DRE(1), MYB (1)
Contig206	ASF 1(1), MYB (2), MYC(4)
Contig208	ASF 1(1), DOF(1), MYB(1), MYB (4), MYC(2), RAV (5)
Contig219	DOF(3), MYB (1), RAV (1)

Contig281	bZIP (1), DOF(4), MYB (4), MYC(4), RAV (4)
Contig282	DOF(2), MYB (3), MYC(2), RAV (3)
Contig288	DOF(3), MYB(1), MYB (5), RAV (6)
Contig304	DOF(1), MYB(1)
Contig374	DOF(7), MYC(2)
Contig395	DOF(6), DRE(2), MYB(1), MYB (7), MYC(4), RAV (3)
Contig437	AGC-box(1), bZIP (1), DOF(6), MYB (6), RAV (3)
Contig477	ASF 1(1), bZIP (2), DOF(4), MYB (1), MYC(6), RAV (2)
Contig498	DOF(8), MYB(2), MYB (7), MYC(6), RAV (3)
Contig522	ABRE(3), DOF(3), ERD1 (4), MYC(4), RAV (1)
Contig542	ASF 1(1), DOF(6), MYB (8), MYC(8), RAV (2)
Contig549	DOF(2), MYB (3), MYC(4), RAV (1)
Contig585	bZIP (1), DOF(6), MYB(1), MYB (2), RAV (2)
Contig596	DOF(2), DRE(3), MYB(1), MYB (5), MYC(2), RAV (3)
Contig597	ABRE(2), bZIP (1), DOF(9), ERD1 (2), MYB (1), RAV (8)
Contig618	bZIP (1), DOF(13), MYB (4), MYC(4)
Contig621	AGC-box(1), ASF 1(1), bZIP(2), DOF(3), DRE(2), ERD1 (2)
Contig635	ABRE(2), ASF 1(1), DOF(8), ERD1 (2), MYB (3), MYC(2), RAV (2)
Contig655	ABRE(2), DOF(7), ERD1 (2), MYC(2)
Contig712	DOF(3), MYB (1), MYC(4), RAV (7)
Contig770	ABRE(1), ASF 1(2), DOF(4), ERD1 (2), MYB(1), MYB (5), SR1 (6)
Contig774	ASF 1(2), bZIP (2), DOF(4), ERD1 (2), MYB(1), MYB (2), MYC(2), RAV (4)
Contig834	ABRE(8), ASF1(2), bZIP (6), DOF(16), DRE(3), ERD1(6), MYB(4), MYB(12), MYC(16), RAV(11), SR1(2)
Contig834b	DOF(2), DRE(2), MYB (2), RAV (2)
Contig843	ASF 1(2), DOF(4), MYB (6), RAV (1)
Contig850	DOF(7), MYB (3), MYC(4)
Contig910	DOF(4), MYC(2), RAV (1)
Contig1007	ASF 1(3), DOF(2), DRE(2), ERD1 (2), MYB (2), SR1 (2)
Contig1131	DOF(6), MYB (7), MYC(22), RAV (3)
Contig1132	DOF(2), MYB (2), MYC(4), RAV (1)
Contig1134	bZIP (3), DOF(3), MYB (5), MYC(2), RAV (4)
Contig1156	DOF(2), MYB (2), MYC(2), RAV (2)
Contig1158	bZIP (1), DOF(3), ERD1 (2)
Contig1165	bZIP (1), DOF(6), MYB (2), MYC(2), RAV (2)
Contig1173	ASF 1(2), bZIP (1), DOF(6), MYB(3), MYB (6), MYC(12), RAV (2)
Contig1173b	DOF(9), MYB(2), MYB (6), MYC(6), RAV (3)
Contig1173c	bZIP (2), DOF(9), MYB(1), MYB (8), MYC(8), RAV (10)
Contig1204	ABRE(1), ASF 1(1), bZIP (1), DOF(4), MYB(2), MYB (3), MYC(4), RAV (3), SR1 (2)
Contig1216	ABRE(1), ASF 1(1), bZIP(2), bZIP (1), DOF(4), ERD1 (2), MYB (4), MYC(2), RAV (1), SR1 (2)
Contig1235	DOF(4), MYB (2), MYC(2), SR1 (2)
Contig1258	DOF(1), MYB (5), MYC(6)
Contig1262	ASF 1(3), bZIP(2), bZIP (1), DOF(3), DRE(1), ERD1 (6), MYB (5), MYC(2), RAV (3)
Contig1266	DOF(5), MYB (4), MYC(12), RAV (3)
Contig1320	ASF 1(1), DOF(7), ERD1 (2), MYB (1), RAV (3)
Contig1338	ABRE(1), ASF 1(2), bZIP (1), DOF(2), DRE(4), ERD1 (2), MYB(1), MYB (10),MYC(6), RAV (2)
Contig1360	DOF(2), MYB(2), MYB (9), MYC(4), RAV (1)
Contig1362	DOF(8), MYB (4), MYC(4), RAV (3)
Contig1367	DOF(3), MYB (2), MYC(2), SR1 (2)
Contig1367b	MYB (1)
Contig1371	bZIP (1), DOF(5), MYB(4), MYB (6), MYC(2), RAV (7)
Contig1396	ASF 1(1), bZIP(2), bZIP (1), DOF(4), DRE(2), ERD1 (2), MYB(2), MYB (9), MYC(6), RAV (3)
Contig1406	ABRE(1), DOF(1), DRE(1), MYB (10), MYC(6), RAV (1), SR1 (2)
Contig1431	bZIP (1), DOF(2), MYB (2), MYC(24), RAV (6)
Contig1471	DOF(3), MYB (2), MYC(6), RAV (1)
Contig1476	DOF(3), DRE(1), RAV (1)
Contig1478	ASF 1(2), bZIP(2), DOF(2), ERD1 (2), MYB (8), MYC(4), RAV (5)
Contig1480	MYC(4)
Contig1489	ASF 1(1), DOF(3), MYB (3), MYC(8), RAV (2)
Contig1539	MYB (1), MYC(2), RAV (2)
Contig1539b	bZIP (1), DOF(1), MYB (1)
Contig1546	DOF(10), MYB (2), RAV (1)

Contig1566	ASF 1(1), DOF(10), ERD1 (2), MYB (2), MYC(4), RAV (2)
Contig1567	DOF(6), ERD1 (2), RAV (1)
Contig1568	bZIP (1), DOF(3), DRE(1), MYB (3), MYC(6), RAV (3)
Contig1580	ABRE(1), bZIP (2), DOF(4), DRE(1), ERD1 (2), MYB (6), MYC(12), RAV (3)
Contig1582	ABRE(2), bZIP (2), DOF(8), ERD1 (4), MYB (2), MYC(10), RAV (9)
Contig1602	ABRE(1), ASF 1(2), DOF(10), ERD1 (8), MYB(1), MYB (3), MYC(4)
Contig1610	ASF 1(1), DOF(7), ERD1 (2), MYB (5), MYC(2), RAV (2)
Contig1627	DOF(3), DRE(1), ERD1 (2), MYB (4)

Drought Stress

Contig	**Transcription Factor**
Contig48	ABRE(3), ERD1(2), MYB(1), MYC(2)
Contig60	bZIP(2), DOF(1), MYB(1), MYC(4), RAV(1)
Contig96	ASF1(1), DOF(3), MYC(2), RAV(1)
Contig105	bZIP(4), ERD1(2), MYB(1), MYC(2), RAV(1)
Contig109	ASF1(1), DOF(1), MYB(1), MYB(4), MYC(2), RAV(5)
Contig125	DOF(4), MYB(2), RAV(2)
Contig141	DOF(6), MYB(3), MYC(4), RAV(3)
Contig144	ASF1(2), DOF(6), MYB(6)
Contig188	bZIP(1), DOF(5), MYB(2), MYC(8), RAV(2)
Contig200	bZIP(1), DOF(9), MYB(1), MYC(10), RAV(3)
Contig221	ABRE(5), bZIP(2), DOF(3), ERD1(4), MYB(2), MYC(4), RAV(2)
Contig228	ABRE(3), bZIP(2), DOF(8), ERD1(2), MYB(1), MYC(8)
Contig261	ABRE(1), bZIP(2), DOF(9), ERD1(2), MYB(7), MYC(4), RAV(12)
Contig298	bZIP(1), DOF(1), DRE(4), MYB(1), MYC(4), RAV(5)
Contig306	ABRE(1), DOF(4), MYC(4), SR1(2)
Contig334	ERD1(2), SR1(2)
Contig350	ABRE(2), DOF(13), ERD1(2), MYB(4), MYC(4), RAV(3)
Contig353	ABRE(1), ASF1(1), DOF(5), DRE(2), ERD1(4), MYB(4), MYC(2), RAV(2)
Contig365	DOF(2), MYB(2), MYB(9), MYC(4), RAV(1)
Contig381	ABRE(4), ASF1(1), bZIP(2), DOF(6), ERD1(8), MYB(17), MYC(4), RAV(1)
Contig482	ASF1(1), bZIP(2), bZIP(1), DOF(4), DRE(2), ERD1(2), MYB(2), MYB(9), MYC(6), RAV(3)
Contig574	DOF(6), MYB(7), MYC(22), RAV(3)
Contig583	DOF(2), DRE(2), RAV(1)
Contig590	DOF(2), MYB(2), MYC(4), RAV(1)
Contig610	DOF(2), MYB(2), MYC(2), RAV(2)
Contig612	bZIP(1), DOF(3), ERD1(2)
Contig618	bZIP(1), DOF(3), MYB(2), MYC(2), RAV(3)
Contig634	DOF(14), MYB(13), MYC(10), RAV(6)
Contig641	bZIP(1), DOF(5), MYB(4), MYB(6), MYC(2), RAV(7)
Contig657	ASF1(1), bZIP(2), DOF(4), MYB(1), MYC(6), RAV(2)
Contig670	DOF(2)
Contig698	DOF(1), MYB(5), MYC(6)
Contig701	ASF1(3), bZIP(2), bZIP(1), DOF(3), DRE(1), ERD1(6), MYB(5), MYC(2), RAV(3)
Contig767	AGC-box(1), bZIP(1), DOF(4), DRE(1), MYB(6), MYC(4), RAV(4)
Contig773	DOF(3), MYB(5), MYC(6), RAV(1)
Contig800	DOF(2), MYB(3), MYC(2), RAV(2)
Contig805	DOF(3), MYB(2), MYC(2), SR1(2)
Contig805b	MYB(1)
Contig867	DOF(15), MYB(1), MYC(6), RAV(11)
Contig885	DOF(3), MYB(2), MYC(6), RAV(1)
Contig887	DOF(1), ERD1(2), MYC(6), RAV(4)
Contig906	ABRE(1), ASF1(2), DOF(8), ERD1(2), MYB(2), MYB(3), MYC(4), RAV(2)
Contig914	ABRE(3), bZIP(2), DOF(3), DRE(2), ERD1(4), MYB(6), MYC(4), RAV(1)
Contig953	ABRE(2), bZIP(2), DOF(8), ERD1(4), MYB(2), MYC(10), RAV(9)
Contig969	ABRE(1), ASF1(2), DOF(10), ERD1(8), MYB(1), MYB(3), MYC(4)
Contig973	ASF1(1), DOF(7), ERD1(2), MYB(5), MYC(2), RAV(2)
Contig1017	bZIP(1), DOF(3), DRE(1), MYB(4), MYC(6), RAV(3)
Contig1055	DOF(9), MYB(1), MYB(5), MYC(6), RAV(4), SR1(2)
Contig1092	ABRE(1), ASF1(3), DOF(3), ERD1(4), MYB(1), MYC(2)
Contig1104	DOF(5)
Contig1115	bZIP(1), DOF(15), MYB(8), MYC(6), RAV(2)

Contig1184	AGC-box(1), bZIP(1), DOF(6), MYB(9), MYC(16), RAV(3)
Contig1184b	ASF1(1), DOF(7), MYB(1), MYC(2)
Contig1184c	MYB(5)
Contig1185	DOF(1), MYB(1), MYB(4), MYC(2), RAV(1)
Contig1185b	DRE(2), MYB(2), SR1(2)
Contig1190	ABRE(1), bZIP(2), DOF(8), ERD1(4), MYB(4), RAV(1)
Contig1195	ASF1(1), DOF(13), DRE(1), MYB(1), MYB(8), MYC(4), RAV(2)
Contig1199	ABRE(1), ASF1(1), bZIP(2), DOF(6), ERD1(2), MYB(5), MYC(2), RAV(2)
Contig1223	ASF1(1), DOF(7), ERD1(2), MYB(1), RAV(3)
Contig1234	ASF1(1), DOF(5), MYB(1), RAV(4)
Contig1239	ABRE(2), bZIP(1), DOF(9), ERD1(2), MYB(1), RAV(8)
Contig1241	DOF(8), MYB(1), MYB(2), MYC(4), RAV(1)
Contig1243	ABRE(2), ERD1(2), MYB(5), MYC(2), RAV(1)
Contig1259	ASF1(1), DOF(5), ERD1(2), MYB(3)
Contig1293	DOF(3), MYB(2), MYB(13), MYC(4), RAV(3)
Contig1304	ABRE(2), DOF(2), ERD1(4), MYB(5), MYC(2)
Contig1326	bZIP(3), DOF(6), MYB(13), MYC(10), RAV(6)
Contig1357	bZIP(1), DOF(9), MYB(2), MYC(2)
Contig1392	bZIP(2), DOF(6), MYB(7), MYC(4), RAV(1)
Contig1408	MYB(2), MYC(2)
Contig1408b	DOF(4), DRE(1), MYB(2), MYB(9), MYC(2), RAV(4)
Contig1447	RAV(1)
Contig1460	DOF(2), MYB(1)
Contig1478	ABRE(1), ASF1(2), bZIP(1), DOF(2), DRE(4), ERD1(2), MYB(1), MYB(10),MYC(6), RAV(2)
Contig1482	bZIP(1), DOF(1), ERD1(2), MYC(2)
Contig1493	ASF1(1), bZIP(2), DOF(8), DRE(1), ERD1(2), MYB(4), MYB(9), MYC(4), RAV(2)
Contig1540	ASF1(3), DOF(3), DRE(2), ERD1(2), MYB(3), RAV(2), SR1(2)
Contig1558	DOF(5), MYB(1), MYB(2), MYC(2), RAV(5)
Contig1579	ABRE(1), AGC-box(1), DOF(3), DRE(2), MYB(1), RAV(2), SR1(8)
Contig1593	ABRE(1), DOF(8), MYB(1), MYB(3), MYC(2), RAV(2), SR1(2)
Contig1613	DOF(3), MYB(4), MYC(6), RAV(2)
Contig1622	DOF(4), MYB(5), MYC(22), RAV(4)
Contig1639b	bZIP(3), DOF(21), MYB(2), MYC(12), RAV(13)
Contig1722	ABRE(1), ASF1(3), bZIP(1), DOF(4), ERD1(4), MYB(6), MYB(11), MYC(10),RAV(4)
Contig1724	ASF1(1), ERD1(2), MYB(1), MYB(3), RAV(1)
Contig1736	bZIP(1), DOF(4), MYB(1), MYB(2), RAV(3)
Contig1770	DOF(5), MYB(1), MYC(6), RAV(1)
Contig1786	ABRE(10), AGC-box(1), bZIP(1), ERD1(6), MYB(1), MYB(2), MYC(6),RAV(2)
Contig1800	MYC(2), RAV(1)
Contig1827	ABRE(1), DOF(2), ERD1(2)
Contig1842	ASF1(1), bZIP(1), DOF(14), MYB(1), MYB(5), MYC(8), RAV(6)
Contig1843	DOF(3), MYB(5), RAV(1)
Contig1868	DOF(15), DRE(2), MYB(10), MYC(4), RAV(5)
Contig1878	ABRE(3), ASF1(3), DOF(2), ERD1(4), MYB(1), MYB(1), RAV(1)
Contig1878b	bZIP(3), DOF(3), MYB(5), MYC(2), RAV(4)
Contig1879	ASF1(1), bZIP(1), MYB(9), MYC(12), RAV(2)
Contig1880	DOF(3), MYB(1), RAV(1)
Contig1942	bZIP(1), DOF(4), MYB(4), MYC(4), RAV(4)
Contig1944	DOF(2), MYB(3), MYC(2), RAV(3)
Contig1950	DOF(3), MYB(1), MYB(5), RAV(6)
Contig1962	DOF(9), DRE(2), ERD1(2), MYB(1), MYB(6), MYC(4)
Contig1967	DOF(1), MYB(1)
Contig2012	MYB(1), MYB(26), MYC(6), RAV(2)
Contig2037	DOF(6), MYB(1), MYC(2)
Contig2049	bZIP(3), DOF(2), DRE(1), MYB(2), MYB(6), MYC(4), RAV(3)
Contig2089	DOF(1), MYB(5), MYC(2)
Contig2171	DOF(8), MYB(2), MYB(7), MYC(6), RAV(3)
Contig2182	AGC-box(1), bZIP(2), DOF(4), ERD1(4), MYB(3), MYC(2), RAV(2), SR1(4)
Contig2190	ABRE(3), DOF(3), ERD1(4), MYC(4), RAV(1)
Contig2214	DOF(2), MYB(3), MYC(4), RAV(1)
Contig2245	bZIP(1), DOF(6), MYB(1), MYB(2), RAV(2)

Contig2268	DOF(2), DRE(3), MYB(1), MYB(5), MYC(2), RAV(3)
Contig2272	bZIP(1), DOF(13), MYB(4), MYC(4), RAV(1)
Contig2284	ABRE(2), ASF1(1), DOF(8), ERD1(2), MYB(3), MYC(2), RAV(2)
Contig2302	ASF1(1), DOF(6), MYB(8), MYC(8), RAV(2)
Contig2310	DOF(4), MYB(2), MYC(8)
Contig2335	ABRE(2), DOF(8), ERD1(2), MYB(2), MYB(3), MYC(6), RAV(4)
Contig2456	MYC(4)
Contig2459	ABRE(1), ASF1(1), bZIP(2), bZIP(1), DOF(2), ERD1(2), MYB(4), MYC(2),RAV(1), SR1(2)
Contig2462	DOF(4), MYB(2), MYC(2), SR1(2)
Contig2495	ABRE(1), ASF1(2), bZIP(1), DOF(5), ERD1(4), MYB(2), MYC(4), RAV(3)
Contig2516	DOF(5), MYB(4), MYC(4), RAV(3)
Contig2531	DOF(5), MYB(4), MYC(4), RAV(3)
Contig2614	ASF1(2), bZIP(2), DOF(2), ERD1(2), MYB(8), MYC(4), RAV(5)
Contig2616	DOF(3), ERD1(2), MYB(9), RAV(1), SR1(2)
Contig2626	ASF1(1), DOF(3), MYB(3), MYC(8), RAV(2)
Contig2654	DOF(3), DRE(1), RAV(1)
Contig2667	DOF(1), MYB(2), MYC(2)
Contig2667b	DOF(2), MYB(1), RAV(1)
Contig2670	ASF1(1), DOF(6), MYB(5), MYC(4), RAV(3)
Contig2727	ABRE(4), ASF1(3), bZIP(2), bZIP(2), DOF(2), ERD1(8), MYB(16), MYC(6),RAV(4), SR1(8)
Contig2747	ABRE(4), ASF1(1), DOF(8), DRE(1), ERD1(6), MYB(15), MYC(8), RAV(3), SR1(2)
Contig2761	ERD1(2), MYB(2), MYC(2), RAV(1)
Contig2782	bZIP(2), DOF(6), MYB(1), MYB(1), MYC(12), RAV(1)
Contig2840	ASF1(3), DOF(4), MYB(1), SR1(4)
Contig2841	ABRE(1), DOF(4), DRE(2), ERD1(2), MYB(3), MYC(2), RAV(3)
Contig2848	ABRE(1), bZIP(3), DOF(6), ERD1(2), MYB(1), MYB(5), MYC(14), RAV(3),SR1(2)
Contig2863	DOF(5), MYB(4), MYC(12), RAV(3)
Contig2882	DOF(9), ERD1(2), MYB(6), RAV(3)
Contig2888	ASF1(1), DOF(3), ERD1(2), MYB(8), MYC(2), RAV(3)
Contig2892	ABRE(1), ASF1(2), bZIP(1), DOF(4), DRE(1), ERD1(2), MYB(1), MYB(3), MYC(4), RAV(2)
Contig2969	MYB(1), MYC(2), RAV(2)
Contig2969b	bZIP(1), DOF(1), MYB(1)
Contig2984	ASF1(1), bZIP(1), DOF(6), ERD1(2), MYB(1), MYB(3), MYC(6), RAV(4)
Contig2989	bZIP(1), DOF(4), MYB(2), MYC(24), RAV(6)
Contig3039	ABRE(2), DOF(6), ERD1(2), MYB(7), MYC(16), RAV(3)
Contig3103	bZIP(1), DOF(2), MYB(2), MYC(24), RAV(7)
Contig3115	DOF(7), ERD1(2), MYB(2), MYC(6), RAV(2)
Contig3121	DOF(5), MYB(4), RAV(1), SR1(2)
Contig1627b	DOF(1), MYC(2)