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Role of Lanc like G protein-coupled receptor-2with BOP and BTB/POZ in Stress Tolerance and High Yielding trait of Pigeonpea

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ABSTRACT

Pigeonpea is drought resilient crop; relatively more drought tolerant than other legume crops. Through detailed evaluation and multi-location trials of cross derivatives, we identified 65 better performing pigeonpea lines. Among these lines, high yielding and stress-tolerant accessions were identified. From our earlier MYB network and flowering genes networks, we could identify tightly linked co-expressinggenes for yield traits. Semi-quantitative expression analyses showed that the defending type drought stress tolerance contributing LAN C like protein GCL-2 is expressed in providing disease resistance and *myb* linked BTB/POZ genes contribute for high yielding of pigeonpea. BOP is a member of BTB group of plant protein. We found differential up-regulation of these genes in drought-tolerant high yielding pigeonpea lines earlier reported by our team. Whereas in another report we explained the *myb* linked expression of BTB/POZ genes. These genes selected from our earlier network analyses were identified, PCR amplified, sequenced and structure validated for its functional domain. Using the gene sequence, we predicted and validated the protein structure of Lan C. The current study extends our earlier findings that these genes are directly taking part in stress tolerance and high yielding traits.

KEYWORDS

Pigeonpea, stress, protein, LanC, gene

INTRODUCTION

Pigeonpea (*Cajanus cajan*) is one of the most common tropical and subtropical legumes cultivated for its edible seeds. Pigeonpea is fast-growing, hardy, widely adaptable, and drought-resistant (Bekele-Tessema, 2007).Pigeonpea can grow on a wide range of soils, from sands to heavy black clays, with variable pH. However, the best pH range is within 5-7. It has a low tolerance of soil salinity, but some cultivars were reported to tolerate high (6-12 dS/m) salinity (Duke, 1983). Because of its drought resistance, it can be considered of the utmost importance for food security in regions where rainfall is unreliable and droughts are prone to occur (Anonymous, 2014).The origin of pigeonpea (*C. cajan*) is either North-Eastern Africa or India (Van Der Maesen, 1989; Ecocrop, 2016). Its cultivation dates back at least 3000 years (Van der Maesen, 1989; Mallikarjuna *et al*., 2011). It isa pantropical and subtropical species particularly suited for rainfed agriculture in semi-arid areas because of its deep taproot, heat tolerance and fast-growing habit (Mallikarjuna *et al*., 2011). Pigeonpea is present in both hemispheres, from 30°N to 30°S and from sea level to an altitude of 3000 m (Ecocrop, 2016). Though sensitive to frost, pigeonpea keeps growing at temperatures close to 0°C and tall plants can survive a light frost. It grows better where annual rainfall is above 625 mm. However, it is highly tolerant of dry periods and, where the soil is deep and well-structured, it continues growing with rainfall as low as 250 to 375 mm. Pigeonpea is sensitive to water logging and salt spray. Under shade growth is reduced and bears thin, pale green foliage and few pods (FAO, 2016).

Sudden climate changes and unavailability of sufficient water supply can severely affect the productivity of agriculturally important crops. Additionally, frequent exposure to environmental stresses such as drought is adversely affecting plant growth and yield. Pigeonpea is cultivated in marginal lands with minimum fertilizer and irrigation facilities making it more vulnerable to water stress during growth and development.Even for short-duration varieties, the yield gets affected due to water stress during early pod development and late flowering stages (Lopez *et al*., 1996). During seed hardening, the crop requires a considerable amount of water and at this crucial stage unavailability of water often causes terminal drought. Despite having deeper roots, drought acts as major yield-limiting factors, especially at critical seedling and reproductive stages of pigeonpea (Saxena, 2008). The onset time, intensity and duration of drought stress can fluctuate during plant growth and yield loss depends on it (Hu and Xiong, 2014). There has been increased progress made in developing drought-tolerant pigeonpea genotypes, but still, it is difficult to meet the conditions arisen due to climate change. It is feasible to develop drought-tolerant varieties through genomics-assisted breeding that would facilitate yield stability under water-deficient conditions (Varshney *et al*., 2014).

As drought is controlled by multigenes, identification of candidate genes and understanding the molecular mechanism associated with drought tolerance in pigeonpea is critical. Many studies have been conducted in model plants to identify candidate genes associated with drought response (Mir *et al*., 2012). In pigeonpea, genomics resources have been developed which can be deployed to identify

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candidate drought-tolerant genes specific to pigeonpea. The pigeonpea genome sequence reported one hundred eleven (111) homologous sequences corresponding to universal drought-responsive protein sequences from the Viridiplantae (Varshney *et al*., 2012). Transcriptome assembly (Kudapa *et al*., 2012), identification of genes for abiotic stresses tolerance of pigeonpea were reported (Sekhar *et al*., 2010;Priyanka *et al*., 2010; Saxena*et al*., 2011; Deeplanaik *et al*., 2013).The present investigation involves identification, sequencing and characterization of proteins with *in-silico* protein structure prediction and domain analyses responsible for stress tolerance and high yielding traits.

MATERIALS AND METHODS

Plant material

Through detailed evaluation and multi-location trials of cross derivatives, we identified 65 better performing pigeonpea lines. Among these lines, high yielding and stress-tolerant accessions were identified.

Drought stress treatment and tissue harvesting

Seeds were treated with surface sterilants and then washed with double distilled water, sown in pots filled with pot mixture with soil collected from field and vermicompost. Plants were grown under controlled conditions. For imposing drought stress, slow drought stress was imposed on plants when they reached 22 days old seedling stage. An exact calculated quantity of water was added to each pot and weighed at regular intervals. Control plants were maintained at 80% relative water content (RWC) throughout whereas, stressed plant growing pots were dried down gradually to 20% RWC. The transpiration ratio (TR)was recorded on a daily basis to calculate the intensity of the drought stress. Stressed plants weredriedthrough transpiration until the TR reached 0.1. Tissues were harvested from the stressed plants. Samples were slightlysmeared using 70% ethanol to remove soil particles. All tissues were immediately frozen in liquid nitrogen and stored at −80°C for RNA isolation.

Preparation of genomic RNA

RNA was isolated from pigeonpea leaves using TRIzol Reagent (Sigma). Quality of sample was checked by agarose denaturing gel (1.2%) and Nanodrop spectrophotometer. First-strand cDNA synthesis is done by Proto script 2nd first-strand c DNA synthesis kit (New England Biolabs) following manufacturers instruction; second strand synthesis and PCR amplification were performed in 20μl reaction mixture using 2ul first-strand cDNA mix. Each reaction mixture contained 2 μL of 10× PCR buffer A, 1.6 μLdNTPs (25 mmol/L), 2 μL anchored oligo and arbitrary primers and 0.2 μL of 4U *Taq*DNA polymerase. PCR reactions were performed using a thermal cycler (G8800ASureCycler 8800 (M/S Agilent) programmed to initial denaturation at 95ºC for 5 min, denaturation at 94 ºC for 30 s followed by annealing at 62 ºC for the 30s, extension at 72 ºC for 1 min for 40 cycles and then followed by final extension at 72 ºC for 5 min.

Cloning and sequence analysis

After completing the amplification process products of *lanC–like GCL-2 protein, bop and btb/poz*amplicons were parted in 1.2 percentagarose gel. Single bands of each gene were expurgated from the gel, eluted and cloned in PCR4-TOPO Vector (Invitrogen) for sequencing. Cloned sequences were blasted with the NCBI BLASTN tool (http://blast.ncbi.nlm.nih.gov) and aligned with earlier reported sequence using CLUSTALW software. Putative encoding region of transit peptides and mature proteins from different plant genomes were predicted using Blast2go (https://www.blast2go.com).

Domain Prediction of lanc-like protein GCL2 and BOP gene in Cajanus

Domain prediction for lanc-like protein GCL-2, BOP gene and BTB/POZ genes has been done by NCBI (https://www.ncbi.nlm.nih.gov/Structure/cdd/wrpsb.cgi) CD-search software. Fasta sequence of BOP gene was retrieved from NCBI (https://www.ncbi.nlm.nih.gov/nucleotide).This blast search explained the diversity in the domain of BOP gene family.

Protein Structure Prediction

RaptorX structure prediction software wasused (http://raptorx.uchicago.edu/) to predict the protein structure. RaptorX gives the appropriate results for the one or multiple distantly related template proteins (especially those with sparse sequence profiles) and quality of the alignment between a target sequence and by a probabilistic-consistency algorithm and a novel nonlinear scoring function. The results obtained were downloaded in graphical form and as their atomic co-ordinate files as well. PROCHECK was used to validate the structure of predicted proteins.

Semi-quantitative PCR

RNA isolation has been done from pigeonpea lines developed by our team with control (Asha, DGRg 55, DGRg 53, DGRg 56 and DGRg 58) plant leaves using TRIzol Reagent (Sigma). Quality of RNA samples was checked by agarose denaturing gel (1.2%) and Nanodrop spectrophotometer.

First-strand cDNA synthesis and semi qPCR amplification

Primer 3 online tool was used to design specific primer for qPCR amplification. Semi qPCR amplification was carried out with KAPA SYBR FAST Universal qPCR Reaction Mix (qPCR Reaction Mix from M/S KAPA BIOSYSTEMS), 1μl cDNA, 12.5 μl Reaction mix and 0.5M of each forward and reverse primers. The volume used for it was made to 25l with nuclease-free water. PCR tubes containing the above components were capped and given a pulse spin to allow proper mixing of the reaction mixture. PCR was carried out in G8800ASureCycler 8800 (M/S Agilent) thermal cycler.

Gel electrophoresis

After completion of qPCR amplification, Samples were loaded in 3.5% metaphor agarose gel and electrophoresed at 90V for 45 min in HE Plus (Hoefer). The gels were stained with ethidium bromide. The resolved amplification products were visualized by illumination under UV light in a gel documentation system (Syngene).

RESULTS AND DISCUSSION

From our earlier MYB network and flowering genes networks, we could identify tightly linked and co-expression of genes for these traits. (Dubos *et al*., 2010; Singh *et al*., 2017).

Semi-quantitative expression analyses showed that the defensin type drought stress tolerance contributing lanc like protein GCL-2 is expressed in providing disease resistance and myb linked BTB/POZ genes contribute for high yielding of pigeonpea (Taddese *et al.,* 2014). BOP is a member of BTB group of plant protein. We found these genes to get expressed together in drought-tolerant high yielding pigeonpea lines earlier reported by our team (Couzigou *et al.,* 2016) whereas in another report we explained the myb linked expression of BTB/POZ genes. These genes selected from our earlier network analyses were identified, PCR amplified and sequenced. From the gene sequence, we have predicted the protein structure and validated it. Lan C was found to be associated with our co-expression analyses. This confirms that these genes are directly contributing to stress tolerance and high yielding traits.

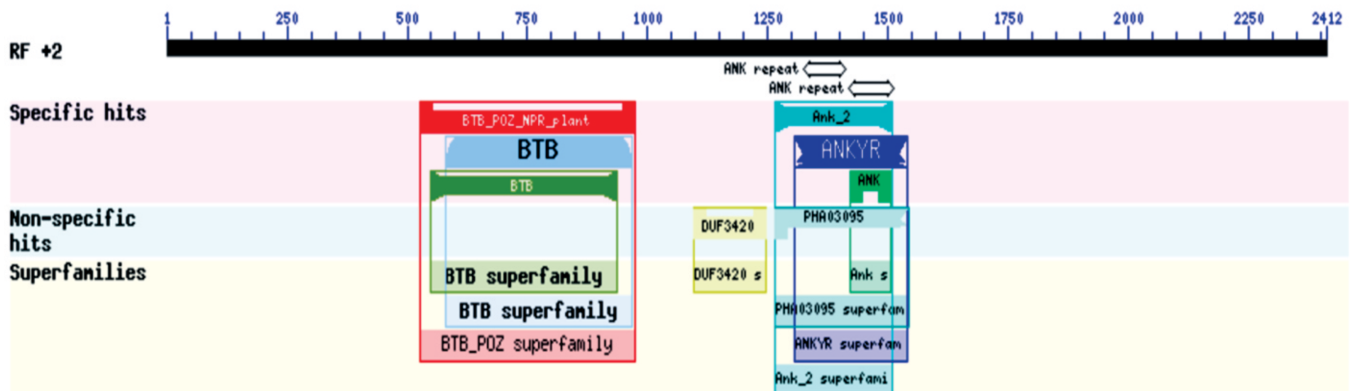

Fig. 1: Domain details of BOP and BTB/POZ proteins

BTB/POZ and TAZ domain-containing protein may act as a substrate-specific adapter of an E3 ubiquitin-protein ligase complex (CUL3-RBX1-BTB) which mediates the ubiquitination and subsequent proteasomal degradation of target proteins (Boyle *et al.,* 2009). BTB/POZ and TAZ domain-containing proteins (Fig. 1) family are essential for female and male gametophyte development and hence contributing for higher seed yield and seed weight. It acts redundantly with BOP2 (Ha *et al.,* 2004). BOP1/2 promote leaf and floral meristem fate and determinacy in a pathway targeting AP1 and AGL24. This mode of action leads to conversion of vegetative to flowering phase, developing more flowers per panicle and higher yield per plant. BOP1/2 act as transcriptional co-regulators through direct interaction with TGA factors, including PAN, a direct regulator of AP1. Controls lateral organ fate through.

BTB/POZ and TAZ domain proteins are Small Ubiquitin-like Modifier (SUMO) ligase act as a substrate specific adapter of an E3 ubiquit in ligase, express ionally related to the SUMO-conjugating enzyme SCE1 (https://www.uniprot.org) and guides the attachment of the small protein SUMO by postranslational modification to target proteins via covalently attached isopeptide bond (Withers and Dong, 2016). It has high similarity to the yeast UBC9 SUMO ligase (Xu *et al.,* 2016). This enzyme exhibited higher sensitivity to ABA in root growth inhibition assays.

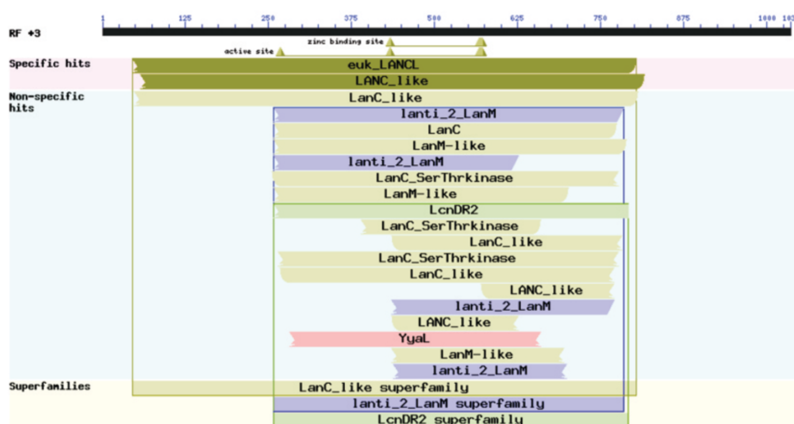

Fig. 2: LAN C protein domain details of *C. cajan*

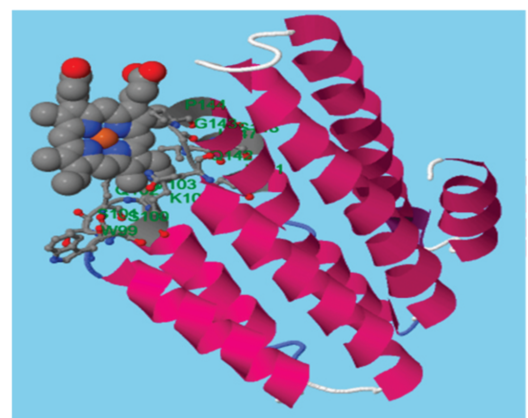

Fig. 3: Predicted structure of LanC like GCL-2 Protein

C. cajan Lan C like GCL-2 protein (Fig. 2 and 3) sequence was submitted to Raptor x Software. Raptor X predicts the secondary and tertiary structure, solvents accessibility, contacts, binding sites and disordered regions of the given input sequence. It is also assigned the confidence scores to determine the quality of the structure. The predicted structure was validated and presented (Fig. 4).

Gene expression analyses

Gene expression analyses were carried out for all selected genes with four selected advanced breeding lines of pigeonpea with control and housekeeping genes (either α-Tubulin or β-Tubulin). Semi-Quantitative results indicating over expression of these genes in selected lines were depicted in figures 5, 6, 7 and 8. For *Ccbt* we could find two variants of the gene.

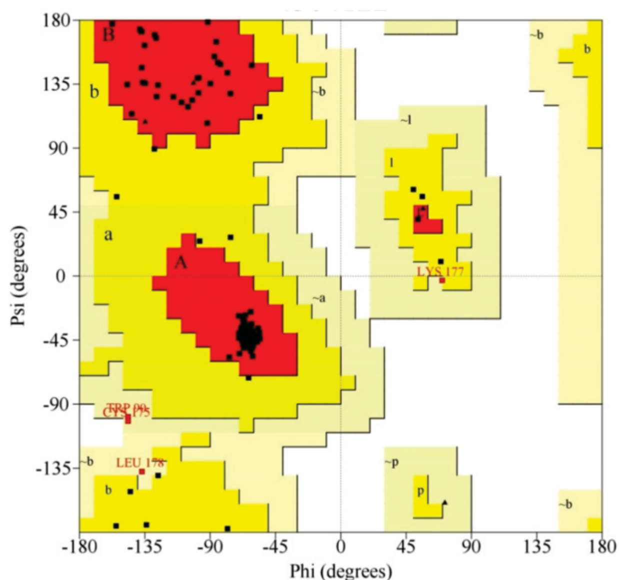

Fig. 4: Ramachandran plot for LANC protein structure validation

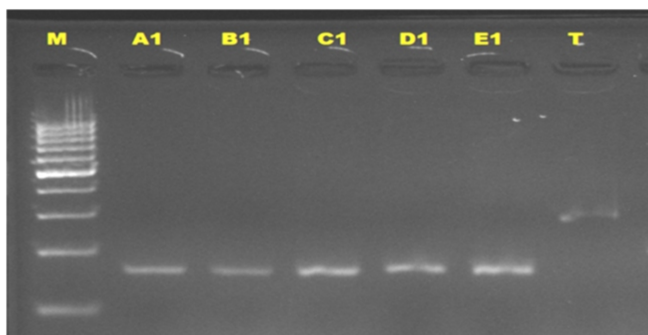

Fig. 5: *Ccbtb* gene expression (Ladder Marker: 100 bp DNA Ladder, Lane A1: Asha, Lane B1: DGRg 55,Lane C1 :DGRg 53,Lane D1: DGRg 56, Lane E1: DGRg 58 and Lane T: α-Tubulin).

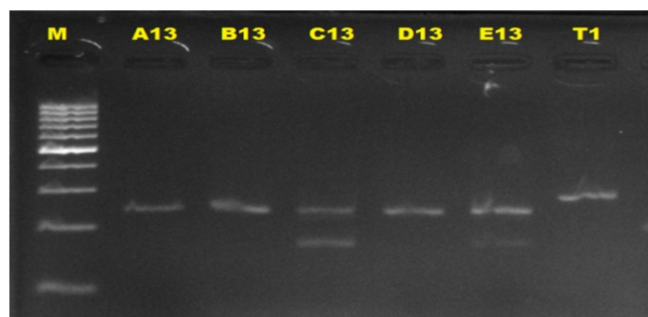

Fig. 6: *Ccbt* (Ladder Marker: 100 bp DNA Ladder, Lane A13: Asha, Lane B13: DGRg 55, Lane C13 :DGRg 53,Lane D13: DGRg 56, Lane E13: DGRg 58 and Lane T1: α-Tubulin)

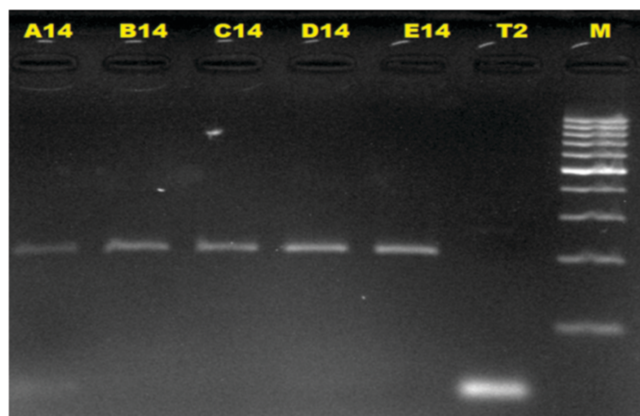

Fig.7: *Ccbop1*(Ladder Marker :100bp DNA Ladder , Lane A1: Asha, Lane B1: DGRg 55, Lane C1 : DGRg 53,Lane D1: DGRg 56, Lane E1: DGRg 58 and Lane T: β-Tubulin)

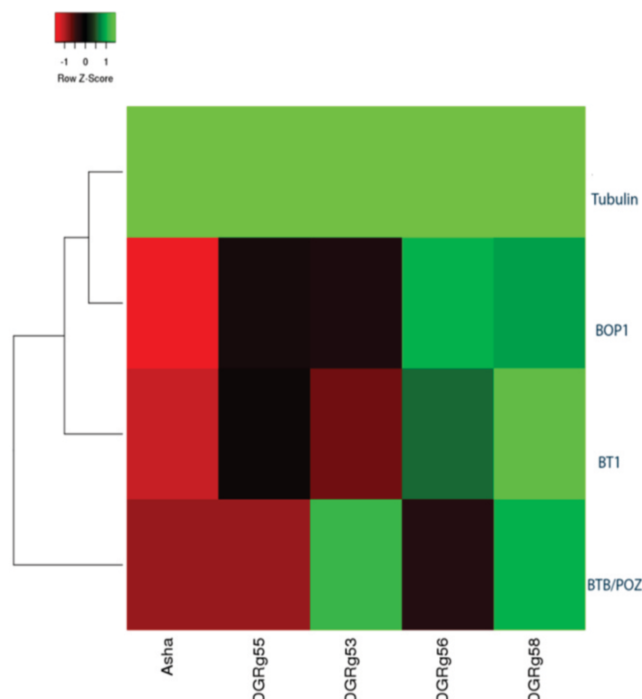

Fig.8: Comparative up and down regulation of genes in different lines of pigeonpea

Gene Network

Predicted gene coexpression network is present in Fig. 9. This co-expression of genes confirms our earlier reports and depicts the network of the gene required by high yielding plants.

BOP Gene

BLADE-ON-PETIOLE 1 (BOP1) and BOP2 encodinggenes are redundant transcription factors restricted to the base of developing lateral organs including the leaf and floral development (Ha *et al*., 2004; Norberg *et al*., 2005; Hepworth *et al*., 2005).

The BOP genes encode proteins containing a BTB/POX VIRUS AND ZINC FINGER (POZ) domain and ankyrin repeat(Ha *et*

Fig.9: Network of genes directly correlated with yield and drought tolerance traits

al., 2007). The *bop1 bop2* mutants display a range of developmental defects, including a loss of floral organ abscission after losing its function. Hence, these are proved to be involved in yield contributing traits manifestation of crop plants. Abscission occurs along specialised cell files, called abscission zones (AZs) that develop at the junction between the leaving organ and main plant body.

ETC gene family

This gene,ENHANCER OF TRY ANDCPC1(ETC1), effects a reduction in trichome formation andan increase in root hair production when overexpressed.Althoughmutations have no detectable effect in awild-type background, they enhance theTRYandCPCmutantphenotypes. These results suggest that ETC1 acts in concertwith TRY and CPC mediate lateral inhibition duringtrichome and root hair development (Kirik *et al*., 2004)

CPC gene family

CPC and TRY inhibit the formation oftrichomes in the shoot and non-hair cells in the root.In both the shoot and root, the final epidermal cell patternappears to result from a lateral inhibition mechanism that isfacilitated by CPC and TRY (Larkin *et al*., 2003; Schiefelbein, 2003). The transcription ofCPC, and perhaps TRYispromoted by TTG and GL1 in the developing trichomes and by TTG and WER in the developing non-hair cells (Lee and Schiefelbein, 2002; Schellmann *et al*., 2002; Schiefelbein, 2003; Wada *et al*., 2002). The CPC and TRY products act in a partially redundant manner to inhibit the neighboring cells from adopting the trichome or non-root-hair fate, possibly by directly moving from cell-to-cell and interfering with the GL1 or WER function(Schellmann *et al*., 2002; Schiefel-bein, 2003).

TCL gene family

TCL2 function redundantly with TCL1 in controlling trichome formation on inflorescences, but they are not fully functional equivalent. Transcription of TCL2 is not controlled by activator complex formed by GL1 and GL3, but MIR156 controlled SQUAMOSA PROMOTER BINDING PROTEIN LIKE (SPL) transcription factors. However, SPLs might require co-activators to regulate the expression of their target genes, including TCL1, TRY and possibly, TCL2 (Gan *et al*., 2011).

RAX gene family

RAX1 is transiently expressed in a small central domain within the boundary zone separating shoot apical meristem and leaf primordia early in leaf primordium development (Keller *et al*., 2006). RAX proteins belong to R2R3 MYB family of transcription factors. RAX1 genetically interacts with CUP-SHAPED COTYLEDON (CUC) genes and is needed for the expression of CUC2 within RAX1 expression domain, suggesting that RAX1 acts through CUC2.The rax1-3 mutants produce fewer flowers and meristems and the rax1-3 rax2-1 rax3-1 triple mutant indicates its central roles in flowering (Keller *et al*., 2006; Müller *et al*., 2006).

TRFL gene family

TRF-like Proteins contribute to the integrity of the nucleoprotein complex known as the telomere cap is crucial for genome stability and for cell proliferation in eukaryotes (Schmitz *et al*., 2002) TRF1 and TRF2 are the only Myb-containing proteins known to bind directly to double-strand telomeric DNA in vertebrates, At least four TRFL genes (TRP1/TRFL1 and TRFL3/TRFL6) reside in regions of the Arabidopsis genome known to be duplicated (Karamysheva *et al*., 2004).

RPT gene family

The RPT2 gene is light inducible; encodes a novel protein with putative phosphorylation sites, a nuclear localization signal, a BTB/POZ domain, and a coiled-coil domain; and belongs to a large gene family that includes the recently isolated NPH3 gene (Sakai *et al*., 2000).

MYC gene family

MYC2 is a key bHLH TF regulating the expression of different subsets of JA-responsive genes (Boter *et al*., 2004; Lorenzo *et al*., 2004; Dombrecht *et al*., 2007). However, MYC2 cannot be the only TF regulating JA responses since myc2/jin1 mutants do not show a complete loss of JA sensitivity. Besides MYC2, several TFs have been shown to be involved in specific aspects of JA-induced responses (Jeifetz *et al*., 2011)

CONCLUSION

The predicted networks of genes were found to be the best for further research. Identified genes and their expression analyses suggest that they could be the best candidates for screening germplasm for variations in identifying donor for crop improvement research.

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