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Identification and characterization of salt-responsive proteins in mango (*Mangifera indica* L.)

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Abstract

Increasing salinity is a cause of concern for meeting UN sustainable development goals and needs urgent mitigation strategies. Extensive use of salinity tolerance rootstocks in salt sensitive fruits are lasting solutions to brutal effects of soil salinization. Polyembryonic mango cultivar 13-1, a salinity tolerant variety from Israel, was used to unravel initial salt adaptive mechanism by imposing salinity screen at 200mM NaCl. Differentially accumulated proteins were separated through 2-D electrophoresis (pH gradient 4.0-7.0), and identified through properties of isoelectric point (pI) and molecular weight by annotation against Citrus isoelectric focusing database. Protein spots (309) were detected on Coomassie-stained gels and about 22 spots were found differentially expressed in control and stress. Overproduction of stress-related proteins like polygalacturonase (97 kDa/4.9PI) and alcohol dehydrogenase (38kDa/5.6PI) is linked to enhanced cell wall integrity, transpiration rate regulation and ionic maintenance in adaptability mechanism. The upregulated phenylpropanoid pathway proteins p-coumaroyl ester, Flavanone3-hydroxylase-2 and UDP-glycosyl transferase are also involved in stress alleviation through flavonoid accumulation. Glutathione S-transferase was also identified with 2.21-fold accumulation in plants exposed to salinity stress, thereby elucidating its role in oxidative stress mitigation. Cell wall and cytoskeleton metabolism related proteins were also found associated with salinity adaptation in mango cv 13-1. Differential accumulation of proteins implicated in signal transduction pathway, transcription regulation and hormone signaling were also identified. Thus, role of differentially expressed proteins under initial salinity stress conditions provide new insights molecular adjustment mechanisms orchestrated by mango rootstock variety by hormone signaling, osmotic arrangements, cytoskeleton modifications, phenol accumulation and transcription regulation.

Key words: Salinity, 2-D Electrophoresis, 13-1, rootstock, signal transduction, phenol accumulation, cell wall and cytoskeleton, transcription regulation.

Introduction

Climate change and soil salinization are major abiotic stresses affecting field performance of agricultural crops and main drivers of impending food scarcity in India and the developing world (Szabo *et al.*, 2016; Kumar and Sharma, 2020). Selection and cultivation of plant varieties that possess inherent or acquired salinity tolerance will address challenges posed by global climate change in near future. Plant adaptation to salinity stress is complex biological phenomenon and involves synergistic regulation of the stress and defence related physiological traits, transcriptional regulation, morphological alterations involving cell wall and cytoskeleton metabolism, oxidative and ionic stress regulatory networks, signal-transduction pathway, *etc.* (Bernstein, 2019). Additionally, salinity stress, which is associated with excessive Na^+ and Cl^- accumulation in the soil, inhibits water and essential mineral absorption from the root zone, due to reduced osmotic and water potential of the soil, thereby derailing the dynamic osmotic adjustments of the plants (Munns and Tester, 2008). Build-up of toxic ions and reactive oxygen species (ROS) in plants (Kim *et al.*, 2008) are known to diminish enzyme activity or even degrade cellular proteins. Deployment of salinity tolerant crop varieties is the most attractive option to overcome the salinity stress. The salinity tolerant plants have inherent or acquired dynamic responses through expression and regulation of complex multigenic traits that leads to their survival under compromised environments (Munns and Tester, 2008). Though all plants try to adjust to adverse soil conditions, the timely and well-coordinated response acquired in tolerant types leads to successful adaptation and hence, survival under stress (Lakra *et al.*, 2018). On the other hand, susceptible types succumb to stress due to their inability to efficiently channelize resources towards osmotic and ionic stress management (Polle, 2015).

Molecular mechanisms employed by plants to combat salinity stress are categorized into responses to initial osmotic and later ionic stress, that include ion transport, ion homeostasis, synthesis of osmo-protectants, ROS regulation, hormone modulation *etc.* (Gupta and Huang, 2014). However, such studies in perennial fruit trees are scarce due to their inherent biological attributes like tree size, life span, use of rootstock, and still there exists gaps in knowledge regarding molecular and regulatory networks operative under salinity stress imposition and their role in plant adaptation. Proteins are involved in plant stress response as structural and regulatory proteins, cellular compartmentalization, post-translational modifications (Kosová *et al.*, 2011). Plant response to salinity is manifested as active ion exclusion or intracellular compartmentation into vacuoles that are associated with enhanced ATP-dependent ion transporters and very well

documented by proteome studies (Peng *et al.*, 2009). Five step stress response process was described by Kosova *et al.*, (2018), wherein proteomic studies distinguished phases of distress and adaptation followed by tolerance, depletion, and recovery of affected plants. Among fruits, mango occupies a special status in tropical and subtropical ecologies in the world, due to abundance in diversity, taste, and legacy. It has been categorized as most salt sensitive among fruit trees (Maas, 1986), displaying stress symptoms like scorched leaf tips and margins, leaf curling, and in severe cases reduced leaf area, leaf abscission, and death of trees (Schmutz and Ludders, 1993). Most of the cultivars are salt sensitive (Bajpai *et al.*, 2017), and variation in ability to tolerate salinity depends on rootstock (Kadman *et al.*, 1976). Gazit and Kadman (1980) reported salinity tolerance in *Mangifera indica* cv. 13-1 and *M. zeylanica* that are recommended as rootstocks. Mango cv. 13-1 was selected as a polyembryonic rootstock for calcareous soils and/or for irrigation with saline water showing good performance as rootstock for 3 cvs. However, there is paucity of transcriptomic or proteomic studies to assign role of gene and protein responses in altered environment. In this study, we aim to identify differentially accumulated proteins during early stress response, in leaves of salt tolerant *M. indica* cv.13-1, by comparing the contrast between control and stressed plants using 2D-PAGE. Furthermore, identified protein spots would be characterized using PI and molecular weight characteristic intrinsic to accumulated proteins using Citrus isoelectric point protein database (http://isoelectricpointdb.org). Eventhough mango polyembryonic rootstocks have been considered salinity resistant, the association of candidate protein families involved in various cellular processes in salt adaptation response have not been studied. The present paper chronicles response of mango rootstock '13-1' to salinity stress by identifying differentially accumulated proteins through 2-D electrophoresis. Identification of differentially expressed proteins was done by annotation with Citrus *ief* database. The study paves way for understanding the behaviour of the rootstock in compromised environment so that it may be utilized in breeding new rootstock varieties.

Materials and methods

Plant materials and growth condition: Seeds of *M. indica* cv.13-1 were sown in polybags containing 8.0 kg of 1:1:1 (w/w/w) mix of soil, sand, and well-rotted farmyard manure and manually irrigated with tap water daily under greenhouse conditions immediately after extraction from fruit. Uniform 6-month-old seedlings were selected based on their vigour, leaf size and were transplanted in 25 cm earthen pot (before salinity stress imposition). Factorial experiment was set up based on randomized complete block design with three replications. Salinity screen was applied by applying @ 200 mM NaCl to one set of pot and changes in soil pH, soil electrical conductivity (EC in dSm^{-1}) was monitored using pH meter and EC meter (Labman Scientific Instruments, India) (EC 4.0dsm^{-1} and pH 8.5). After 15 days, fourth leaf from the control and treatment was taken, quickly wrapped in aluminium foil, frozen in liquid nitrogen and stored at -80°C until further use.

Two-dimensional (2D) polyacrylamide gel electrophoresis: Two-dimensional gel electrophoresis was used to separate isolated crude protein s using isoelectric focusing (IEF) gel in the first dimension and SDS PAGE in the second dimension. 10 µL of each sample was loaded on the 1D gel for normalization of the protein concentrations. The IEF was performed with 300µg of each sample using 18 cm Immobilized pH gradient (IPG) strips (GE Healthcare Life Science, Sweden) with 4 to 7 linear pH gradients. Electrophoresis was carried out as per protocol described by Duan *et al.*, (2013). The IPG strips were then incubated in the equilibration buffer (Glycerol 30% (v/v), 50 mM Tris-HCl (pH 8.8), 6 M Urea and 2% (w/v) SDS and 2% (w/v) DTT) for 15 minutes. Subsequently, SDS-PAGE was performed in the second dimension. The equilibrated strips were transferred to 10% Acrylamide SDS-PAGE gel for electrophoresis at 150 V for 1 hour. The experiment was conducted with three replicates in each case.

Extraction of total protein from the leaf: Total proteins were extracted from the leaves of control and stressed plants using Phenol method slightly modified from (Carpentier *et al.*, 2005). One gram of leaf powder was suspended in 5.0 mL of cold extraction buffer (5 mM EDTA, 1% DTT, 50 mM Tris-HCl (pH 8.8), 100 mM KCl and 30% sucrose). An equal volume of ice-cold phenol solution was added and the solution was mixed by vortexing. The phenol phase was collected after centrifugation (12,000 x g, 30 min at 4 °C) and precipitated with 5 volumes of 100 mM ammonium acetate in methanol overnight at 4°C. The protein pellet was washed with 1% DTT and air-dried and resuspended in 100 µL lysis buffer (4% (w/v) CHAPS, 1% (w/v) DTT, 7 M Urea and 2 M Thiourea) and stored at -80°C until further use. The protein concentration was calculated using the Bradford protein method using bovine serum albumin serving as the reference standard (Bradford, 1976).

Image and data analysis: The gel was stained with Coomassie blue, digitized using Epson Expression 11000XL Scanner and analysed using the Progenesis SameSpot software (Totallab Ltd, UK). The spots were detected, matched, and normalized with default parameters. Differentially expressed protein spots among the control and stress samples were ascertained using normalized spots and compared with the reference gel. The fold difference and p-value were calculated using one-way ANOVA. The threshold value for fold change was set at 2.0 for up and downregulation at $P \leq 0.05$.

Result and discussion

2 DE reveals differential accumulation of proteins: Salinity tolerant, polyembryonic mango cultivar 13-1, displayed accumulation of 309 proteins spots in control and salinity stress plants. The protein spots showed a broad distribution in the pI (4.0 to 7.0) and mass (10 to 250 kDa) respectively. Furthermore, 69 (22.33%) protein spots were identified with significant difference 2-fold change (up or down) between control and stress (Fig.1), and 22 spots (31.88%) were showing significant differences ($P \leq 0.05$) and a 2-fold change (Fig. 2). These were based on spot intensity variations among control and treated samples quantified by SameSpot (version 5.1.012) software. Among the 22 differentially accumulated proteins, 14 and 8 were up and down-regulated respectively under saline conditions (EC:>4.0dsm^{-1} and pH 8.5) after 15 days of stress imposition. Molecular weight (kDa) and PI values of 22 differentially accumulated spots was calculated and compared with *Citrus sinensis* proteome (close relative of *Mangifera* based on sequence homology) isoelectric focusing database (http://isoelectricpointdb.org). The identified protein sequences were used to conduct protein-translated nucleotide

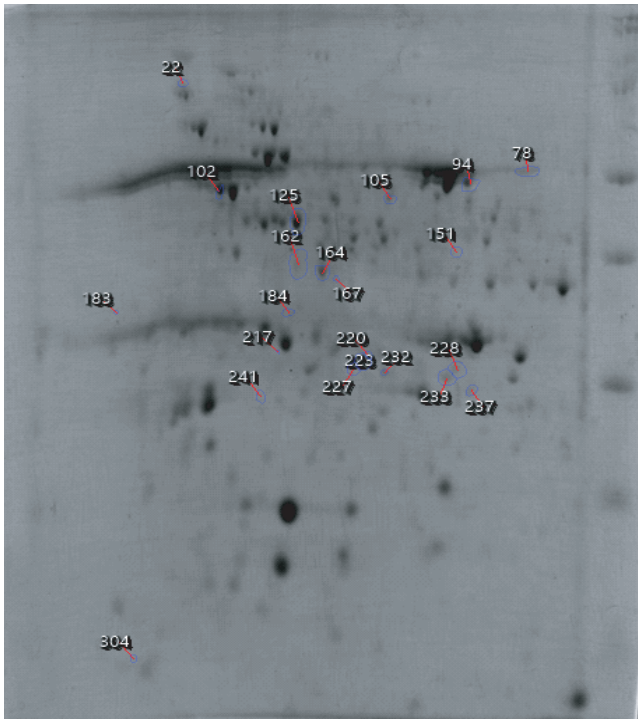

Fig 1. Two-dimensional electrophoretic pattern of soluble leaf proteins obtained from NaCl-treated plants of mango cv. 13-1. Protein spots identified based on the significant difference ($p<0.05$) and ≥2 fold protein change in abundance (up or down) from the control plants and are indicated with a number.

(tblastn) against *Mangifera indica* (Taxid: 29780) (https://www.ncbi.nlm.nih.gov), which yielded 74 hits, that were used for identification of proteins based on maximum query coverage and total score. Two spots were left uncharacterized (Spot 183 and 304), as their sequence did not match with *Mangifera indica* translated sequences.

Salinity-responsive proteins in mango: Salt-responsive protein species were identified and assigned to different pathways related to stress perception, adaptation through ion accumulation, ROS mitigation, signal transduction pathway, cell wall and cytoskeleton metabolism, transcriptional regulation, and protein metabolism based on sequence homology and domain similarity (Fig. 3) and are described as follows:

Stress and defense: Two (10%) polypeptide sequences assigned spot # 22 and 162 displayed upregulation (2 and 2.51-fold) matched with polygalacturonase (PG53) and alcohol dehydrogenase (Adh), complete cds respectively.

The accumulation of polygalacturonase promotes sustained cell wall integrity and transpiration rate under salinity stresses. The functional role of Adh in protecting plants during osmotic and ionic stresses is well documented (Su *et al.*, 2020).

Signal-transduction pathway: Functional categorization of protein spots from 2D gels placed 5 spots (#78, 94, 125, 164, and 227) in category of signal transduction, which has importance for perception of environmental signals and transmission to cellular machinery for activating adaptive responses. Spot 227 was up-regulated while the remaining 4 spots (78, 94, 125, and 164) were down-regulated. Spot 227 was up-regulated with fold change 5.3 and annotates with

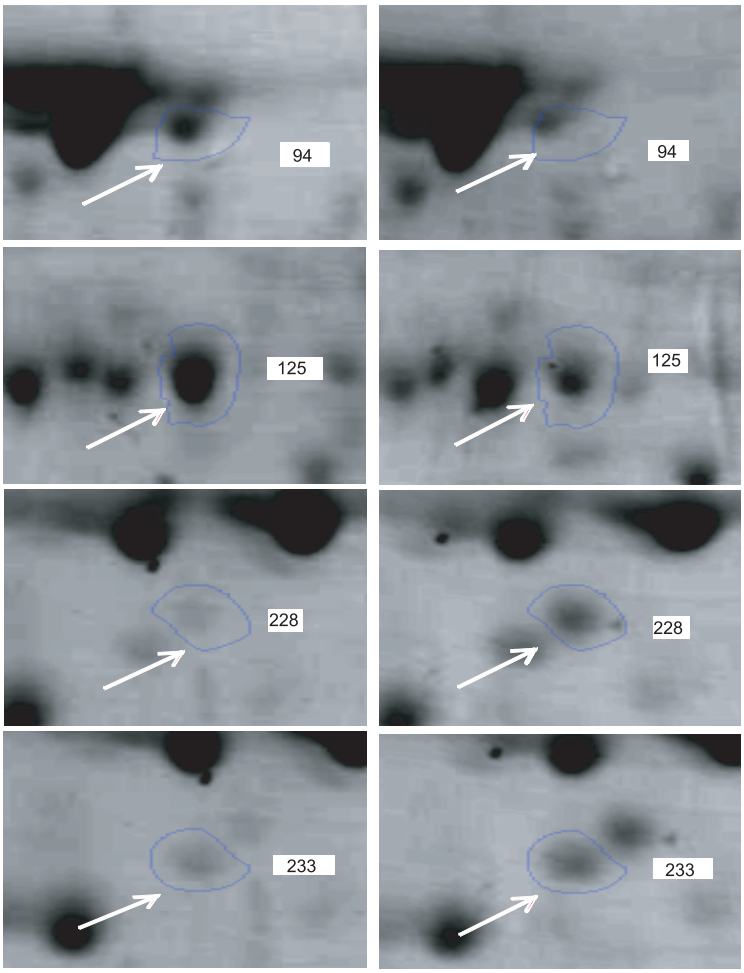

Fig 2. Close up view of protein spots showing a significant difference ($p<0.05$) and ≥2-fold change between control and NaCl-treated plants as obtained in Fig.1 (# 94: RLK; #125: LRK; #228: MYB; #233: PGP2).

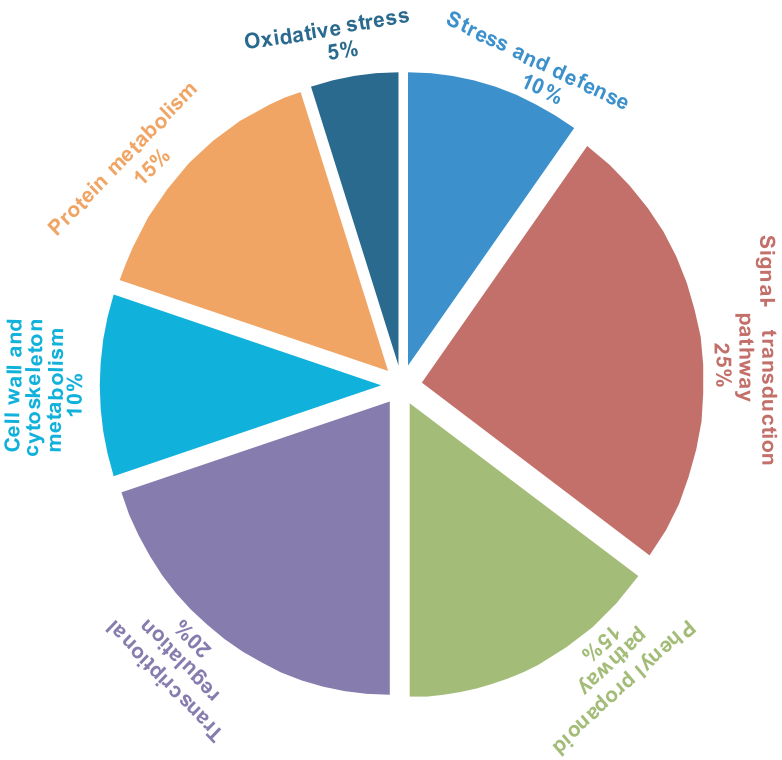

Fig 3. Functional categories of salinity-responsive protein identified by annotation with Citrus IEF database.

Table 1. Identification of differentially expressed Salinity-responsive proteins in mango cultivar 13-1

Spot Number	Differential expression (Control vs Stress)	MW KD/PI	Protein	Sequence coverage (%)	Accession	Pathway
22	Up	97/4.9	Polygalacturonase (PG53) gene.	3%	MK936586.1	Stress and defense
162	Up	38/5.6	Alcohol dehydrogenase 2mRNA.	100%	GU233767.1	
78	Down	56/6.4	NBS-LRR resistance protein gene.	34%	HQ243443.1	Signal-transduction pathway
94	Down	53/6.4	F6N15.8-like protein mRNA, partial cds (receptor-like protein kinases (RLKs)	11%	AF370123.1	
125	Down	43/5	Receptor-type protein kinase LRK gene.	37%	AY693370.1	
164	Down	38/5.8	Receptor-type protein kinase LRKgene, partial.	42%	AY693370.1	
227	Up	27/6	Putative leucine-rich repeat protein gene.	67%	AY776277.1	
167	Up	36/6	p-coumaroyl ester	100%	KF956018.1	Phenyl propanoid pathway
184	Up	32/5.7	Flavanone3-hydroxylase-2 (f3h2) mRNA.	91%	KF929410.1	
217	Up	29/5.6	UDP-glycosyl transferase (UFGT).	94%	KY386896.1	
105	Down	47/6	MibHLH2 mRNA for basic helix-loop-helix.	14%	LC529415.1	Transcriptional regulation
167	Up	36/6	AP2	57%	MH759782.1	
220	Up	28/5.9	CRT/DRE-binding factor (CBF1) mRNA.	41%	KM373347.1	
228	Up	27/6.4	MiMYB3 mRNA for MYB transcription factor.	49%	LC529413.1	
232	Down	27/6.2	CRT/DRE-binding factor (CBF1) mRNA.	22%	KM373347.1	
241	Up	23/5.3	Small GTP Rab11 (rab) mRNA.	99%	KF768564.1	Hormone signaling
233	Up	26/6.4	P-glycoprotein2 (PGP2) mRNA.	95%	KM096529.1	Cell wall and cytoskeleton metabolism
102	Down	45/5	Actin7(ACT7) mRNA.	91%	HQ586000.1	
151	Up	40/6.4	eukaryotic initiation factor	94%	MK002430.1	Protein metabolism
223	Down	28/6	expansin1mRNA.	86%	AY600964.2	
241	Up	23/5.3	Heat-shock protein	93%	KJ459859.1	
237	Up	25/6.5	Glutathione S-transferase UDP.	92%	KX061499.1	Oxidative stress

leucine-rich receptor-like kinases (LRR-RLKs), that are important candidates for imparting salinity and ABA tolerance through ROS scavenging activity and MDA reduction (Wang *et al.*, 2017). These receptor like protein kinases located at plasma membranes regulate salinity and oxidative stress with overproduction as revealed in our data (Table 1). Spot #78 corresponding to NBS-LRR is a class of protein is disease-resistance proteins that may serve as receptors for detecting osmotic and oxidative stresses induced by drought (Honda *et al.,* 2018). The protein identified by spot #94 represents F6N15.8-like mRNA for receptor-like protein kinases (RLKs) that are known as the major gene family of conserved signaling components, with 747 members identified in potato, respectively. These are serine/threonine protein kinases, associated as plasma membrane proteins, wall-associated kinases (WAKs) linked to the pectin fraction of the cell wall, cytoplasmic-type RLKs localized mainly in cytoplasm, *etc.* (Ye *et al.,* 2017). Likewise, spot 125 and 164, display down regulation and represent Lectin receptor kinases (LRKs) that are localized in plasma membrane systems and their over expression is known to impart salinity tolerance through ROS scavenging activity and osmotic adjustments through activation of water channels or Na^+ transporters.

Phenylpropanoid pathway: Total 3 Spots #167, 184, and 217 displaying overproduction in plants exposed to salinity stress were placed in phenylpropanoid pathway that gives rise to polyphenols. Plant phenolics play an important role in adaptation to challenging environments like drought and salinity and their accumulation is consistent with stress conditions. In general, these secondary metabolites have an antioxidant property that ameliorates plant performance under stress. The protein spot 167 represents p-coumaroyl esters, and it's corresponding up-regulation reveals an enhanced synthesis of lignin, the phenylpropanoid polymer located at the linocellulosic cell wall responsible for enhanced mechanical strength and imperviousness to pathogen invasion (Takeda *et al.*, 2018). Likewise, spot 184 denoted the Flavanone3-hydroxylase-2 and #217 represents UDP-glycosyl transferase (UFGT), the flavonoids imparting stress tolerance in mango (Sharma *et al.*, 2019).

Transcriptional regulation and protein metabolism: Transcription factors are key regulatory elements that affect gene expression in response to specific signals, including environmental stresses such as salinity. The proteomic database

identified 4 spots, 105, 232, 220, and 228 that showed similarity to transcription regulators like bHLH, CBF-DREB, MYB *etc.* The protein spot 105 represents the *Mi*bHLH2 and spot 232 represents C-repeat (CRT)/dehydration-responsive element that is implicated in abiotic stress tolerance (Xie *et al.*, 2019). While protein spot 228 denotes MYB transcription factor, and its over expression in rice plants showed increased tolerance to drought and salt stress accompanied by accumulation of osmolytes and enzymatic antioxidants (Tang *et al.*, 2019). Total of 3 spots (15%) namely, 151, 241, and 223 were placed in this group. Further, spot 151 represents the eukaryotic initiation factor 1A (eIF1A) that has role of stress response regulator to improve plant salt and osmotic stress tolerance via regulation of associated enzymes and ROS scavenging, thereby reducing cell damage under stress conditions. (Li-shu, *et al.*, 2019). Likewise, protein spot 241 represents the Heat-shock protein that acts as chaperone, is induced by numerous stresses and has pivotal role in stress response module through association with ROS (Khan *et al.*, 2019). The protein spot 223 denotes expansin-1, the EXP-A and EXP-B proteins are required for the cell extension and developmental processes of cell wall modification. (Zhang, 2021).

Cell wall and cytoskeleton metabolism: Overproduction of protein Actin7(ACT7) represented by spot 102 recorded the importance of cell cytoskeleton, cytoplasmic streaming, cell shape determination, cell division, organelle movement, and extension growth in salinity stress. (Wang *et al.*, 2011). Cytoskeletal proteins like Actin filaments are important components in salt stress tolerance in *Arabidopsis* (ACT7) isovariant plays an important role in regulating the moderate-high temperature response in Arabidopsis root (Sumaya *et al.,* 2021).

Oxidative stress: Only a single spot #237 was identified that represented Glutathione S-transferase, and has precise involvement in oxidative stress protection. The role of Glutathione S-Transferases in combating abiotic stresses, including arsenic detoxification in plants is well documented (Kumar *et al.*, 2018).

Molecular weight and isoelectric focus point characteristics of differentially accumulated proteins were annotated with the Citrus IEF database, which established the role of oxidative stress mitigation, enhanced cell wall integrity, transpiration rate regulation and ionic maintenance to be important attributes for adaptability mechanism. Flavonoid upregulation and cytoskeleton metabolism-related proteins were also found associated with salinity adaptation in mango cv. '13-1'. These proteomic based insights illustrate salinity adaptation mechanisms in mango rootstock through stress perception, signal transduction and morpho-physiological alterations. Similarly, corroboration of 2DE outputs through peptide mass fingerprinting techniques would establish response and adaptation mechanisms of salinity stress that will fast track rootstock breeding in fruits.

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