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Research Article

OVERVIEW OF CELLULAR AND MOLECULAR RESPONSES TO ABIOTIC STRESSES IN FRUIT CROPS

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Abstract: Abiotic stresses are major challenges affecting yield and production in plants including fruit trees. Drought, salinity, high temperature, frost are the major problems in tropical and subtropical ecosystems wherein major fruit orchards are concentrated. The review presents current scenario and understanding on the mechanism of abiotic stress responses in fruit crops. An overview of the physiological, biochemical and molecular changes that occur upon confronting stress is also presented. The details of the genes involved in stress response, native adaptation mechanism in natural ecosystems are also highlighted. Several abiotic stress pathways, trehalose biosynthesis genes, signal perception and transduction mechanisms are described. Insights into biochemistry of ROS, their production sites, antioxidant defence systems working in concert to control the cascades of uncontrolled oxidation to protect from oxidative damage are also covered. Opportunities and scope for stress breeding in fruits to re-establish homeostasis in stressful environments can be key to changing climate conditions.

Keywords: *Abiotic Stress, Adaptive, Cellular and Molecular Response, ROS, Trehalose*

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Introduction

Global agricultural production systems are prone to serious threats of changing climatic scenario and the severity of this peril is fuelled by other challenges like abiotic and biotic stresses. Among the abiotic stresses that affect crop plants, three major abiotic factors such as drought; salinity and high temperature are responsible for crop losses worldwide. On the other hand, climate change is predicted to cause an increase in average air temperature of between 1.4ºC and 5.8ºC, increasing atmospheric CO_2 concentration and significantly altering rainfall pattern [17]. Recent estimates envisage cumulative average yield loss of >50% in major crop plants primarily due to drought, salinity and high temperature [8]. In perennial fruits major setback assigned to abiotic stresses *viz*., drought, salinity, elevated temperature, frost and flooding is drastic loss in yield and productivity. Tropical and subtropical fruits responsive to climatic variables in different geographical locations and crop adaptations have evolved varied mechanisms of stress responses. Although substantial work has been done with regard to abiotic stress mitigation in cereals and annual crops, there are only sporadic reports available in perennial fruit trees [1, 7]. Earlier studies have clearly demonstrated morphological, physiological, biochemical and molecular changes under stressed environments [13]. Owing to large canopy, geographical adaptation and environment factors, symptom expression vary with the trees, genotypes, age and inherent tolerance/susceptibility factors. This review describes some aspects of stress induced changes with particular emphasis on biological pathways, gene expression and transmission of protein signals related to abiotic stresses.

Sustainable production of Fruit crops in changing climate scenario

India is the second largest fruit producer (44.04 million tonnes) and changing temperature regimes is known to affect fruit produce in Citrus, grapes and melons. Similarly high temperature regimes cause more runner production at the expense of strawberry fruits. Specific chilling requirements are keys for fruiting in litchi, pome and stone fruits. Low production of citrus and banana due to climate vagaries are testimony to temperature and rainfall stresses. High temperature and moisture stress also increases sunburn and cracking in apples, apricot and cherries and increase in temperature at maturity will lead to fruit cracking and burning in litchi [25]. Thus, adverse weather conditions, abiotic stresses pose serious threat to growth, development and reproduction in all fruit crops.

Natural adaptive mechanisms in stress tolerant plants

Plants including fruit trees grow in a dynamic environment wherein there are constantly forced to face several abiotic and biotic stresses, which affect their growth and development. A list of commonly known example of species and their geographical adaptations to various extremes (drought, hot, cold *etc.*) are given below in [Table-1] which also describes their morphological adaptations. Plant species have interestingly evolved distinct mechanisms to adjust, adapt, overcome, recover and produce substantial yield even at stressful environments. Some common morphological and physiological mechanisms exhibited by stress tolerant plant species are:

Drought adaptation: Drought tolerant plants respond to potential dehydration, and exhibit number of morphological features such as leaf drop, xeromorphic leaf structure, leaf or stem succulence and produce deep tap roots to reach water from deep aquifers or ground water table [15].

Heat tolerance: Heat or high temperature tolerant plants have good heat-regulating mechanisms at high temperatures. Transpiration cooling phenomenon operates to prevent evaporation losses when plant is most likely under water deficit conditions through stomatal closure and synthesis of a specific class of heat shock proteins which may function to protect enzymes that would be denatured by the excess heat.

Cold acclimation: In temperate regions, plants produce more unsaturated membrane fatty acids to maintain membrane fluidity needed for transport proteins. Most plants withstand cold or frost by dropping fragile parts prior to the cold onset, and enter dormancy, by lowering water content in cells. Furthermore, cold acclimateion is enhanced in plants with antifreeze proteins that retard growth of ice crystals within cells.

Table-1 *Description of plant structural and behavioural adaptations to natural stressful ecosystems*

Adaptations	Plants	Morphological manifestations
Xerophytic adaptations (Xerophytes)	Cactus, Pinophyta belongs to conifers, Ammophila	Needle shaped leaves providing lesser surface area to minimize evaporation, maximum water uptake, hair layers to conserve trapped moisture
Grassland adaptations	Grasses, Asclepias, Echinacea (coneflower)	Deep roots, narrow leaves, flexible stems which bend with wind
Tundra adaptations	Mosses, low growing plants and small berry plants	Small statures plants, dark colored flowers, heat loving
Rainforest adaptations (Mesophytes)	Bamboo, mangrove, epiphytes (bromeliads) and orchids	Slide shaped leaves lets rain run-off so fungus doesn't grow on plants, deep growing roots anchor the plant to prevent it from washing away.
Temperate forest adaptations	Quercus, Fagus, Betula	Generally possess thick bark which serves as water storage organs
Water adaptations (Hydrophytes)	Nymphaeaceae, Nelumbonucifera, Anthoerotopsida	Air pockets in stems at leaf base helps in floatation

Table-2 *Classes of metabolites and hormones regulating stress responses in plants*

Metabolites and hormones	Type of stress involved	References
Proline, glycine-betaine, and other compatible osmolytes	Drought, salinity and dehydration	[43]
Reactive oxygen species (ROS) and malondi-aldehyde	Both biotic and abiotic stresses	[17]
Abscisic acid, jasmonic acid, salicylic acid, polyamines	Drought, Salinity and Cold	[29]
Phenolic compounds (coumarin, lignin, flavonoids, tannins, isoflavonoids)	Pathogens, Oxidative stress and UV-light	[11,26]
Unsaturated fatty acids	All environmental stresses	[42]

Table-3 *Probable mechanisms of stress responses in different fruit crops*

Plants	Abiotic stress	Adaptation mechanism	Process involved in stress adaptation
Malus domestica	Cold	Acclimation	Dormancy
Psidium guajava	Freezing	Acclimation	Thick cuticle, epicuticular wax, Three sub-epidemically layers of compact cells, high amount of esclerídeos.
Poncirus trifoliata, *Citrus sinensis*	Cold	Moderate tissue tolerance	Cell wall modifications, presence of dehydrins (LEA proteins)
Fragaria ananassa	Salt and drought	Tolerance	Osmotic adjustment
Vitis vinifera	Heat	Thermo-Tolerance	Accumulation of glycine betaine

Table-4 *Abiotic stress responsive gene classes characterized through functional genomics*

SN	Genes	Gene Action/Function	Crop	Tolerance Acquired	References
1	*At*DREB1A	Transcription factor	Arabidopsis, Tobacco	Drought, Salinity	[23]
2	CAP2	Transcription factor	Citrus, Tobacco	Salinity	[38]
3	DREB	Transcription factor	*Arabidopsis thaliana*	Salinity	[22]
4	Pyroline-5-carboxylate reductase	Proline synthesis	*Arabidopsis thaliana*, Carrot	Drought and Salinity	[10,32, 39]
5	Aquaporins	Membrane pore proteins.	*Citrus sinensis*, Banana Grapevines	Drought	[42]
7	HSP	Heat shock proteins	Tomato	Heat	[34]
8	COR	*Cold regulated genes*	*Arabidopsis thaliana*	Cold	[9]
9	T(FT)	Transcription factor	Litchi	Cold	[39]
10	ATG3	Autophagy-related protein MdATG3s	Apple	Tolerance to all kinds of stress	[42]
11	PIP	Plasma membrane intrinsic protein genes	Citrus, Tobacco, *Arabidopsis*	Drought	[2,20,35,44]
12	*TPS1* and *TPS2*	Trehalose synthesis	Tomato	Drought, salt and oxidative stress and cold tolerance	[18, 21]

Cold acclimation in guava appears to be a multifactorial process involving complex physiological and biochemical changes and also overlapping responses with drought stress [14].

Salinity tolerance: High levels of salts in soil and water affect water potential and decrease water absorption by plant roots. At high sodium concentration plants produce organic solutes for distribution in root cells that maintain more-negative water potential to facilitate water movement from soil into the root. Another modification observed in halophytes, which live in saline soils is presence of active salt glands in leaf epidermal cells that excrete salt. Furthermore, arid halophyte Nolana, has salt glands that are used to obtain water which condenses on leaf surface and facilitates active transport of water into the leaf tissues.

Physiological and biochemical changes induced by abiotic stress

Abiotic stresses namely drought, low temperature, and salinity have negative impacts on plant growth and development. These stresses cause a range of physiological responses in plants such as stomata closure, suppression of cell growth and photosynthesis, and ultimately respiration. Stomata closure occurs progressively with a parallel decline in net photosynthesis and water-use efficiency and also changes in photosynthetic pigments. Recent studies demonstrated that leaf cuticle and surface wax serves as an important trait for multiple stress tolerance, and many regulatory genes coordinate phospholipid and galactolipid accumulation [26]. Homeostasis regulation of ROS in crop plants *i.e.* coordinated function of regulation networks to maintain ROS at non-toxic levels by delicate balancing act between ROS production, and ROS-scavenging pathways is critical in stress physiology [16]. Production of osmoprotectants, sugar alcohols and heat shock proteins are the major responses of stress induction. Proline, an osmolyte that is synthesized from l-glutamic acid through D1-*pyrroline*-5-*carboxylate* (P5C) by the action of two enzymes: P5Csynthetase and P5Creductase. In contrast, *proline dehydrogenase* and P5C dehydrogenase are the enzymes that degrade proline to l-glutamic acid. In response to water deficit, P5C synthetase is induced and *proline dehydrogenase* is repressed, resulting in a net accumulation of proline. Late embryogenesis abundant genes, abbreviated as LEA genes, are developmentally programmed for expression in desiccating seeds and they encode small hydrophilic proteins that are predicted to protect proteins and membranes conferring dehydration tolerance during drought and salinity stress. Apart from these, genes responsive to abscisic acid, rubisco, helicase, glutathione-S-transferase (GST), and carbohydrate metabolism are also triggered during drought and salinity [4,16,], having pivotal roles in influencing plant response to stress [Table-2].

Reactive oxygen species (ROS) and antioxidant enzymes

Scavenging of reactive oxygen species (ROS) by enzymatic and non-enzymatic systems, cell membrane stability, expression of aquaporins and stress proteins are critical mechanisms of abiotic stress tolerance which are described below. The production of ROS (*viz.*, oxygen ions, free radicals and peroxides) results in oxidative collapse which is an early event of plant defence response to biotic as well as abiotic stress. During drought and salinity, ROS levels increase dramatically resulting in oxidative damage to proteins, DNA and lipids [3, 12].The ROS such as singlet oxygen, hydrogen peroxide, superoxide anions, hydroxyl radicals, can strongly attack membrane lipids and increase lipid peroxidation [29]. The consequences of lipid peroxidation, protein degradation and DNA fragmentation eventually leads to cell death. Drought-induced high production of ROS increases the content of malondialdehyde (MDA), which serves as an indicator of oxidative damage [31]. Low-molecular mass antioxidants (glutathione, ascorbate) and ROS-scavenging enzymes {superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), ascorbate peroxidase (APX)} [3] and non-enzymatic antioxidants collaborate to keep the integrity of the photosynthetic membranes under oxidative stress. O_2- can be dismutated into H_2O^2 by (superoxide dismutase (SOD), in the chloroplast, mitochondrion, cytoplasm and peroxisome. POD plays a key role in scavenging H2O2 which was produces through dismutation of O_2^{-} catalyzed by (superoxide dismutase (SOD). CAT is a main enzyme to eliminate H_2O_2 in the mitochondrion [40]. The capability of antioxidant enzymes to scavenge ROS and reduce the damaging effects thus correlates with the drought resistance of plants.

Abscisic Acid and LEA Proteins: Abscisic acid initiates gene transcription for additional water conservation measures on the part of the plant and has a control on the regulation of LEA proteins (late embryogenesis proteins). LEA proteins occur naturally in maturing seeds as they desiccate for dormancy. The LEA proteins help to stabilize the membranes and other proteins of the dehydrated cells, but LEA genes can also help plants grow better during drought. They have been reported to have relevance with drought, salinity and cold tolerance [4, 19, 27].

Heat shock proteins: Heat-shock proteins (Hsps)/chaperones are responsible for protein folding, assembly, translocation and degradation in many normal cellular processes, stabilize proteins and membranes, and can assist in protein refolding under stress conditions. They are found to play a crucial role in protecting plants against stress by re-establishing normal protein conformation and thus cellular homeostasis.

Molecular responses and genes involved in abiotic stress tolerance in fruit crops

Plants exhibit mechanisms to overcome continued exposure to stress which in turn leads to signal transduction ultimately resulting physiological and metabolic responses in the form of stress responsive gene expression [30]. Numerous genes with diverse functions are induced or repressed by abiotic stress [46], a list of which with special emphasis for fruit crops are presented in [Table-4]. Most of the genes belong to the category of transcription factors which are secondary messengers that induce gene expression of major stress responsive genes.

Genetic manipulation of abiotic stress tolerant genes for functional validation

Even though transgenic strategies are not being used to produce abiotic stress tolerant plants due to the modalities and issues related to transgenics, the genes identified through transcriptome and genome sequencing projects are to be functionally validated through genetic transformation in model systems say tobacco or Arabidopsis. For instance, genes encoding organic osmolytes, heat shock proteins, plant regulators, late embryogenesis abundant proteins and transcription factors responsible in activating gene expression [5] offers scope for functional validation. Genes encoding proline, glycinebetaine polyamines, mannitol, trehalose and galactinol acquired for osmotic protection [33,41] have potentials for conferring dehydration and salinity tolerance in crop plants [6,13]. An efficient transformation and regeneration system forms the key of success in functional validation of the novel or known genes of stress responsiveness.

Molecular breeding for abiotic stress tolerance in fruit crops

Molecular markers and breeding for abiotic stress tolerance using markers are the simplest alternative to reduce the breeding cycle. From transcriptome and genome data, markers linked to abiotic stress tolerance genes/traits may be identified through co-localization and genetical genomics studies which would help in marker assisted selection. In guava [14], cold acclimation and drought tolerance in cv Ruby Supreme, was found due to 17.4 kDa dehydrin accumulation and anthocyanins. Lucknow-49 also exhibited moderate freezing tolerance. In another experiment conducted by Abounoid and co-workers [1] on 40 landraces of guava subjected to in vitro polyethylene glycol (PEG) treatment, drought tolerance at 8% PEG concentration could be detected in all the landraces. Using ISSR and SRAP markers, drought tolerance and susceptible landraces could be discriminated in their study. In mango [7] peroxidase enhanced stress tolerance in polyembronic mango cultivar Nekkare was reported that can be used as pre-breeding materials or as rootstocks [Table-5].

Table-5 List of abiotic stress tolerant varieties of few fruit crops that are used as root stocks

SN	Crop	Varieties/Cultivars	Stress response
1	Mango	Bapakkai, Nekkare, 13-1, ML2, ML6	Salinity tolerant
2	Guava	Sardar	Salinity tolerant
3	Grape	Dogridge	Salinity tolerant
4	Lime	Rangpur Lime and Cleopatra mandarin	Salinity tolerant
5	Annona	Arkasahan	Drought tolerant
6	Pomegranate	Ruby	Drought tolerant
7	Fig	Deanna, Excel	Drought tolerant

Conclusion and future line of work

In the present context of climate change, development of stress tolerant varieties or cultivars in fruit crops have become paramount which can suffice wider adaptability and also sustain abiotic stresses. The major focus of abiotic stress tolerance is: i) to identify climate resilient genomes for coping with climate changes and, ii) breeding abiotic stress tolerant rootstock cultivars in fruit crops. In the present review, we have presented the status of research progress made in understanding the abiotic stress tolerance mechanism in plants. There is also a need to understand how different combination of stresses trigger the specific enzymes involved in the targeted metabolism, as well as the possible networks that coordinate the plant adaptations to stresses. Recent progress made in omics approaches like fluxome, exome, also needs to be coupled with the abiotic stress physiology and molecular biology studies so as to get real time status of stress tolerance mechanism.

Application of research: Abiotic stress tolerance in fruit crops needs to be elucidated for developing stress tolerant plants. The molecular mechanism underlying stress resilience can be used for selection procedures.

Research Category: Horticulture

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