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Mechanism of Salt Tolerance in Fruit Crops: A Review

P.K. Nimbolkar[1], Jyoti Bajeli[2], Arunima Tripathi[3], A.K. Chaubey[4], N.M. Kanade[5]

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ABSTRACT

Salinity in soil and water is a critical factor that is causing hindrance in crop production under salt affected areas. Plant metabolic activities are apparently restricted due to accumulation of salt. The event of salt stress happens to be the reason of severe alteration in the sequence of plant growth and development which ultimately reduces the survivability of plants. The physiological and biochemical mechanisms of tolerance to various osmotic and ionic components of salinity stress are evaluated at the cellular, organ and whole plant level. The course of adaptation towards salinity stress could be of various types such as avoidance, exclusion, extrusion, ion compartmentalization *etc*. Appropriate understanding of mechanism involved in salt tolerance at different levels in plant tissues provide a new opportunity to integrate physiological and biochemical knowledge to improve the salinity tolerance of fruit crops, especially from the nutritional aspect. Such information not only helpful in escalating the productivity in salt affected areas, but also facilitate in bringing relatively more salt affected areas under cultivation.

Key words: Adaptation, Fruit crops, Salinity, Tolerance mechanism.

In the global scenario of climate change, environmental stresses like salinity, drought, flood, heat are not only plundering cereal crops, but also affecting the production of fruit crops, worldwide. The burgeoning population is becoming a challenge to farmers and researchers, as they have to produce 70% more food for an additional 2.3 billion people by 2050 (Hasanuzzaman *et al*., 2013). To achieve the target of inflating food demand, crop losses due to various environmental stresses have to be minimised (Shanker and Venkateswarlu, 2011). Among these stresses, salt stress is one of the important aspects which can be mitigated by exploiting the nature of salt tolerance of fruit crops.

Salt-affected soils comprise of abundant amount of salt concentrations (NaCl, $MgSO_4$, KNO_3 and $NaHCO_3$) that influence the plant growth and development, soil structure, water quality and other use of land as well as soil resources. In India, approximately 6.75 million hectare (mha) area is occupied by salt-affected soils (including coastal) out of which 1.71 mha land is under saline soils and 3.79 mha land is under alkali soils (ICAR-CSSRI, 2016). The extent of distribution of salt-affected soils is relatively more in the arid and semi-arid regions as compared to the humid regions. Northern India is the largest belt of mango cultivation bearing sufficient salt content as a result of introduction of canal irrigation which has become a serious issue for the establishment of new mango orchards (Dubey *et al*., 2007).

Salinity in soil or water is one of the major component which severely constrains the crop production and acting as a major threat to the capacity of agriculture to sustain the increasing population. Flowers (2004), Munns and Tester (2008) Parida and Das (2005) and Shannon (1998) stated that high salinity affects plant by water stress, ion toxicity, nutritional disorders, oxidative stress *etc*. (Zhu, 2007). There are various salts active in soil salinization among which salts of several cations i.e., sodium (Na^+), magnesium (Mg^{2+}), calcium (Ca^{2+}) prominently induce salinity to soil, however, sodium is the dominant salt causing deterioration of the physical structure of the soils (Chaitanya *et al*., 2014). Plants have the capacity to evolve several mechanisms for salt tolerance like avoidance, osmotic adjustment, Na^+ exclusion from leaf blades, Cl^- excluder from roots or leaves and tissue tolerance (Munns and Tester, 2008). In fact, osmotic tolerance involves the plant's ability to tolerate the drought aspect of salinity stress by maintaining leaf expansion and stomatal conductance (Rajendran *et al*., 2009). The increasing area under salt affected soils is becoming a major obstacle in crop cultivation due to which production per unit area is gradually decreasing. Such area can be brought under the cultivation of perennial fruit crops, which bear the exceptional quality of salt tolerance. In this manner, the waste land can be utilized to increase the productivity along with ensuring food and nutritional security to people of India.

[1]College of Horticulture & Forestry, Central Agricultural University, Pasighat-791 102, Arunachal Pradesh, India.
[2]Department of Horticulture, College of Agriculture, Govind Ballabh Pant University of Agriculture and Technology, Pantnagar-263 145, U.S. Nagar, Uttarakhand, India.
[3]Section of Horticulture, RMD CARS (IGKV), Ambikapur-497 001, Chhatishgarh, India.
[4]Department of Soil Science, Banda University of Agriculture and Technology, Banda-210 001, Uttar Pradesh, India.
[5]Division of Fruit Crops, Indian Institute of Horticultural Research, Bengaluru-560 089, Karnataka, India.

Corresponding Author: Jyoti Bajeli, Department of Horticulture, College of Agriculture, Govind Ballabh Pant University of Agriculture and Technology, Pantnagar-263 145, U.S. Nagar, Uttarakhand, India. Email: jyoti.bajeli24@gmail.com

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Information on the salt tolerance mechanism is useful for identifying and developing cultivars as well as rootstocks that increase the scope of adaptability to saline environment and can be further utilized for expanding cultivation of fruit crops under saline areas. Moreover, identification of salt tolerant rootstocks and performance of scion cultivars on those rootstocks in saline conditions will determine the success and expansion of area of fruits like mango in salt affected soils (Dubey *et al*., 2007).

Concept and consequences of salt stress in relation to plant growth and development

Potential challenges confronted by cultivating plants in excess salinity are osmotic regulation, ion transport and toxicity. Many researchers (Hasegawa, *et al.*, 2000; R. Munns, 2002; Zhu, 2007) have stated that salinity beyond a certain limit escalates water stress, ion toxicity, nutritional disorders, oxidative stress, alteration of metabolic processes, membrane decomposition, genotoxicity, reduced cell division and expansion. All these factors collectively affect the plant growth, development and survival. Osmotic stress caused due to the physiological drought, lowers the osmotic potential and consequently leads to reduction of cell growth, root growth and shoot growth that also induces inhibition of cell expansion and reduction in cell wall formation (Chaitanya *et al*., 2003). Toxicity of ions (Na^+ and Cl^-) damages the function of nutritional equilibrium and disrupts the cell organelles and their metabolism. Therefore, inhibition of salinity in plant growth is the result of osmotic and ionic effects. Schematic summary of effect of salinity stress on plant growth is shown in Fig 1. Munns (2002) elaborated the effect of salinity into two phases (Fig 2) in which the first phase is osmotic stress which results as a rapid and intense response of increase in external osmotic pressure caused due to increase in NaCl levels in the medium, contributing to a stronger reduction in growth. The second phase is ionic phase that leads to slower response as a result of toxic ion accumulation in tissues. Such condition induces severe toxicity in leaves, represented by chlorosis and emergence of necrosis in these tissues. Leaf injury and death is probably due to the high salt load when the cells exceeds the scope of salt compartmentation in the vacuoles, accumulation of salt starts to build up in the cytoplasm of toxic leaves (Munns *et al*., 2008). Osmotic stress and toxicity of ions trigger foliar injury in different fruit crops depicted in Fig 3.

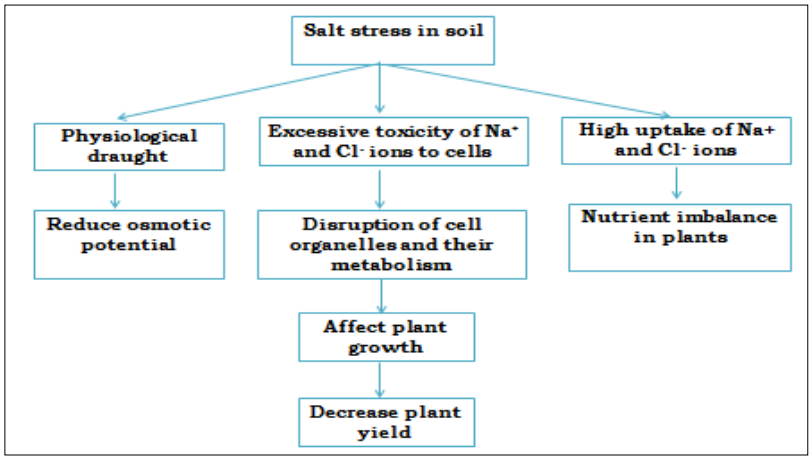

Fig 1: Schematic summary of salt stress effect on plant growth and development. (**Source**: Evelin *et al*., 2009)

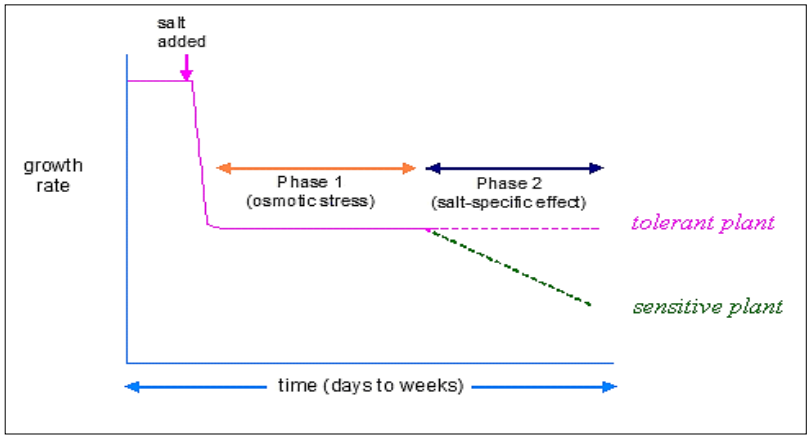

Fig 2: Response of plant to growth phases under salt stressed conditions. (Source: Munns, 1995).

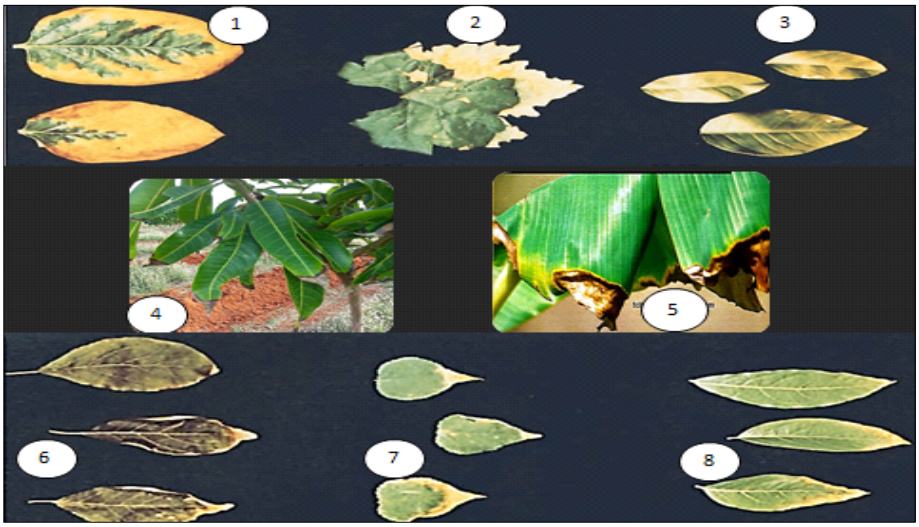

Fig 3: Salt injury symptoms on leaves of different fruit crops:
1-Apple; 2-Grape; 3-Grape fruit 4-Mango; 5- Banana; 6- Plum; 7-Apricot; 8- Avocado (Source-Bernstein, 1980).

Mechanism of salt tolerance

The mechanism concern with the salt tolerance is genetically controlled and it varies from plant to plant and species to species. The degree of salt tolerance may upsurge or decline depending on the environmental factors and/or plant species. The procedure involved in salinity tolerance is salt avoidance, salt-exclusion, salt-extrusion, salt dilution, ion compartmentalization and so on. Salt avoidance is the systematic procedure of removal of deleterious salt ions from the plant parts. The ability of salt exclusion by plant is supported by low net Na^+ uptake by cells in the root cortex that helps in removal of Na^+ ions from the leaf area (Davenport *et al*., 2005). The exclusion of Na^+ from the roots assures that Na^+ does not accumulate in toxic concentrations within leaf blades. The shortcomings in exclusion of Na^+ manifests its toxic effect after days or weeks, depending on the species and causes premature death of older leaves (Munns and Tester, 2008). This mechanism of exclusion prevents the entry of salt while allowing the water to pass through it, boosting maximum salt removal. Under high salinity stress, concentration of Na^+ appears to reach a toxic level before Cl^- does in plant tissue and likewise most studies have concentrated on Na^+ exclusion and the control of Na^+ transport within the plant (Munns and Tester, 2008). Pandey *et al*. (2014) reported that mango rootstock 'Olour' had the highest potential to check the translocation of Na^+ and Cl^- ions in leaf tissues, while 'Kurukkan' had the maximum proficiency to reduce upward movement of Na^+ ion from its roots while, 'Terpentine' also had an ability to decrease both Na^+ and Cl^- ion translocation from the roots. Green-Way and Munns (1980) correlates the salt tolerant nature of citrus with its ability to prohibit toxic ions to enter into shoots. Though, citrus is a salt sensitive crop, certain rootstocks like Rangpur lime (*C. limonia*) and Cleopatra mandarin (*C. reshmii*) act as Cl^- excluders (Cooper, 1961; Cooper and Gorton, 1952; Walker *et al*., 1983; Zekri and Parsons, 1992). Whereas, Trifoliate orange (*Poncirus trifoliate*) and its hybrids are recorded to be Na^+ excluders (Grieve and Walker 1983) and *C. macrophylla* act as 'B' excluder (Embleton *et al*., 1962). Salt-extrusion involves role of different salt excreters to remove salt via glands or bladders or cuticle found on leaf surface. Excess salt absorbed from soil is dumped in salt glands that facilitate the plants to become adaptable in saline environments. The mechanism involved in salt dilution targets the maintenance of succulent characters in different plant tissues. Plants achieve this by increasing their storage capacity with the development of thick, fleshy, succulent structures. Succulence emerges as a result of vacuoles of mesophyll cells filled with water and increase in their size. This mechanism is controlled by regulating the dilution capacity of plant tissues. Plants cannot withstand high salt concentration in their cytoplasm. Hence, plants transfuse the excess salt either into vacuole or sequester in older tissues which are eventually sacrificed, thereby, protecting the plant from salinity stress.

Ion compartmentation of salt in different plant parts generally occurs at the organ as well as cellular level. At organ level, higher degree of salt compartmentation takes place in roots as compared to shoots. At cellular level, excess salt is compartmentalized mainly in cytoplasm and hence, this mechanism act as a protection gear for various enzymes

Table 1: Crops tolerant to certain levels of salinity.

Crop	Range of tolerance	Reference
Date palm	Highly Tolerant	Furr and Ream, (1968)
Natal Plum	Highly Tolerant	Bernstein *et al*., (1972)
Guava	Moderate tolerant	Patil *et al*., (1984)
Fig	Moderate tolerant	Patil and Patil, (1983)
Indian jujube	Moderate tolerant	Hooda *et al*., (1990)
Pineapple	Moderate tolerant	Kulkarni *et al*., (1973)
Olive	Moderate tolerant	Taha *et al*., (1972)
Pomegranate	Moderate tolerant	Patil and Patil, (1982)

that are occupied in the mesophyll cells of leaf (Munns and Tester, 2008). Troncoso *et al.* (1999) studied that salt stress arises due to NaCl in different grape rootstocks. They categorised these rootstocks on the basis of their tolerance nature; sensitive (41 B, R. Lot, 110 R, 140 R and 161-49), moderately tolerant (13-5 and Ramsey) and tolerant (196-17, CH-1, CH-2 and Superior) and suggested that tolerance level of *in vitro* grown rootstocks to NaCl levels appears to be due to their capacity to accumulate more amount of salt, increase in K concentration in the tissue and maintenance of high water level.

The compartmentalization of ions is a consequence of ion homoeostasis (Fig 4). Restricting the intensity of ion concentrations across the plant to sustain a constant environment inside the cell is referred as 'Ion Homeostasis'. Transportation of various ions inside the plant is manifested through distinct ion selective channels/transporters, symporters, antiporters and carrier proteins present in the plasma membrane of the root cells which allow the displacement of specific ions within the cell and regulate the ionic balance under saline condition. Schroeder *et al.* (2013) justified that transportation of Na^+ and K^+ is regulated by Na^+/K^+ symporter *i.e.* HKT 1 symporter which is found in the plant cell membrane removes excess Na^+ from xylem and hence protect the photosynthetic apparatus from Na^+ toxicity. Salt Overly Sensitive (SOS) pathway of homeostasis is triggered by the activation of the receptor in response to salinity and transcriptional induction of genes by indicating the intermediate compounds (Sanders, 2000). In this pathway, calcium binding proteins SOS3 explicitly comes in contact SOS2 and stimulates a serine/threonine protein kinase (Liu and Zhu, 1998; Halfter *et al.*, 2000). This SOS3 activates the SOS2 on the cell membrane, while SOS2-SOS3 complex phosphorylates SOS1, a Na^+/H^+ antiporter on cell membrane that excludes Na^+ outward the cell (Quintero *et al.*, 2002; Guo *et al.*, 2004). When concentration of Na^+ gets excessive in cytosols, the Na^+/H^+ antiporters help to maintain the imbalance by transporting the surplus amount of Na^+ into vacuolar space and make it compartmentalized (Blumwald, 2000). The exchange of Na^+/H^+ in vacuole is regulated through two separate proton pumps, *i.e.*, vacuolar H^+-ATPase and vacuolar H^+-translocating pyrophosphatase V-PPase (Blumwald, 1987).

Role of Osmoprotectants, Polyamines and Hormones for Salt tolerance

Proline (osmolite) accumulation can act as a selection criteria for tolerance of most species in stressed conditions (Parida and Das 2005; Ashraf and Foolad 2007; Ahmad *et al.,* 2009) and it acts as ROS scavenger and $1O_2$ (singlet Oxygen) quencher (Smirnoff and Cumbes 1989; Matysik *et al*. 2002). Supplements of proline encourages salt tolerance in olive tree by modulating some antioxidative enzyme activities, photosynthetic activity and thus, retained better plant growth and water status in olive trees (Ahmed *et al.*, 2010). Glycinebetaine execute a protective role against salt stress (Chen and Murata 2008). The primary function of glycinebetaine during salinity stress is osmotic adjustment (Gadallah 1999), protein stabilization (Makela *et al.,* 2000), protection of photosynthetic apparatus (Allakhverdiev *et al.*, 2003) and reduction of ROS (Ashraf and Foolad, 2007). Foliar application of glycinebetaine at critical stages (e.g., prior to spring frosts) may protect plants and emphasizes yield. Moreover, it also increased leaf area, leaf weight and photosynthetic rate (Mickelbart *et al.,* 2006). Compatible solutes involved in the protection of enzymes from denaturation promote the membrane stabilisation and act as an adaptation mechanism by facilitating osmotic adjustment (Ashraf and Foolad, 2007). With respect to salinity or drought, accumulation of soluble carbohydrates in plants has been widely reported, despite a significant decrease in net CO_2 assimilation rate (Murakeozy *et al.*, 2003). In a situation of salt stress, gradual assembling of carbohydrates in the form of glucose, fructose, sucrose, fructans, trehalose and starch takes place in the tissues (Parida *et al.*, 2002). Trehalose is a sugar that acts as a

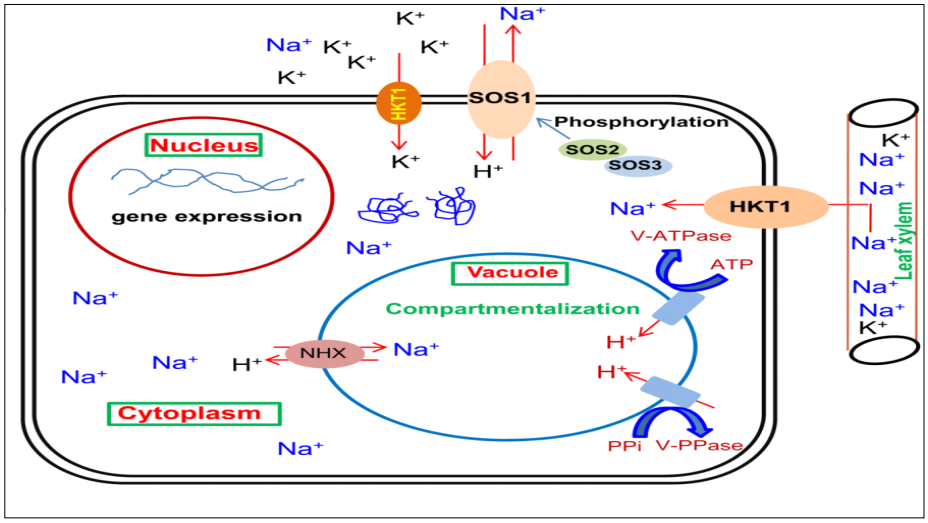

Fig 4: Compartmentalization of ions (Na^+) during ion-homoeostasis (Source: Priyanka *et al.*, 2015).

consistent solute and regulated in plants during abiotic stress (Zeid, 2009; Lopez-Gomez and Lluch, 2012). Exogenous application of trehalose alters transcript levels of transcription factors involved, cell wall modification, nitrogen metabolism and genes related to stress and defence mechanisms well as those of fatty acid biosynthesis (Bae *et al*., 2005). Pandey *et al*. (2014) observed that trehalose concentration increases as a result of increase in salinity levels in olour and Kurukkan. It plays an osmoprotective role in physiological responses, enhancing the plant's tolerance to abiotic stress. Singh *et al*. (1987) briefed that proteins participate as an important agent in osmotic adjustment. Protein accumulates in plant during salt stress and provides a storage form of nitrogen which is re-utilized later on. It can be synthesized *de novo* as a mechanism against salt stress or may be available in constitutively fewer concentrations (Pareek and Grover, 1997).

Polyamines (PAs) such as putrescine (Put), spermidine (Spd) and spermine (Spm) are organic polycations present in all living organism which perform various developmental processes (Tonon *et al.,* 2004). Relevant information on exogenous application of polyamines is available that mitigates salinity damage by enhancing endogenous polyamines, reducing ROS, improving photosynthesis, improving K: Na ratio and promoting plant nutrient status. Various studies (Shen *et al*., 2000; Bouchereau *et al.,* 1999; Capell *et al*. 2004; Kauskabe *et al*. 2004) also highlighted that exogenous application of polyamines to stress treated cells act as a remedy to injured cells and supplements growth promotion which differs among the plant species. Amri *et al*. (2011) revealed that foliar application of spermidine and putrescine polyamines discourages the effects of salinity in pomegranate (*Punica granatum* L.) cv. 'Rabbab'. Among different grape rootstocks under excessive NaCl condition, putrescine, spermine and spermidine contents showed a consistent increase. While, putrescine increase was highest in St. George, spermidine and spermine were found maximum in the Dogridge and Salt Creek which indicates the ability of salt tolerance of these rootstocks (Upreti, 2010).

Abscisic acid (ABA), being a stress hormone, not only plays a significant role in response to various abiotic stresses and indicator of stress condition but also associated with various physiological processes like seed dormancy, leaf senescence, acceleration of closing of stomata, synthesis of storage proteins and lipids and so on (Tuteja, 2007). Various findings concluded that major functions of ABA are regulation of water balance and osmotic stress tolerance in plant tissues. It is a well known fact that ABA performs a remarkable function of cellular signalling that mediates the expression of a number of salt and water deficit-responsive genes. Numerous authors (Cramer and Quarrie, 2002; Kang *et al*., 2005; Cabot *et al*., 2009; Atkinson and Urwin, 2012; Babu *et al.* 2012) in their research have affirmed an increase in the level of ABA in plant leaves under stress condition. Jeschke *et al*. (1997) and Fricke *et al.* (2004) confirmed that exposure of plant roots to salt solution activates the ABA in roots to that triggers ion accumulation in vacuoles. This may be essential for adaptation under saline conditions since it further increases water potential as well as uptake of water under salinity stress. Jamalian, *et al.* (2013) disclosed that exogenous application stimulates the mechanism of antioxidant defence and provide appropriate condition for the growth and yield attributes in strawberry ('Queen Elisa' and 'Kurdistan') under moderate salt stress. Upreti and Murti (2010) observed higher ABA content during salt stress in Salt Creek and Dogridge, popular salt tolerant rootstocks of grape. Moreover, plant hormones other than ABA such as gibberellic acid (Ahmad *et al.*, 2009), Jasmonic acid (Hossain *et al*., 2011), Brassinosteroids (Houimli *et al.,* 2010; El-Mashad and Mohamed, 2012; Hayat and Ahmad, 2011) associated with various metabolic processes like reduction of lipid peroxidation in the leaves, senescence, stomatal closure, yield enhancement, stimulation of plant growth under stress and so forth. Such hormonal studies have been executed mostly in vegetables and cereals. Therefore, in order to alleviate the deleterious impacts of salinity, there is an urgent need to investigate the hormonal interactions and their effectiveness under salt stress condition in perennial fruit crops as well.

ROS signalling and adaptation under stress condition

Plants carry a potential behaviour to adapt in a particular environment, depending upon the environmental conditions, bring about developmental changes among them. Probable environmental stresses such as deficit or excess of water or light, low or high temperature, high salinity, pathogen attack and others cause adversely affect plant growth and development by inducing various metabolic changes like appearance of an oxidative stress (Diaz-Vivancos *et al*., 2008; Hernández *et al*., 2004a, b). During the course of salt stress, plants up-regulate the production of reactive oxygen species (ROS) such as; H_2O_2 (hydrogen peroxide), O_2^- (superoxide), $1O_2$ (singlet oxygen) and OH (hydroxyl radical). Excessive production of ROS leads to lipid peroxidation, protein degradation and DNA mutation (McCord, 2000, Wang *et al*., 2003; Vinocur and Altman, 2005; Pitzschke and Hirt, 2006). (Miller *et al*., 2010; Barba-Espín *et al*., 2011) reported that ROS perform a key role in plants as signal transduction molecules that control stimuli of stress. An anitoxidative system (enzymatic and non-enzymatic) efficiently governs the ROS production. While, the non-enzymatic ROS scavengers include ascorbic acid (ASC) and glutathione (GSH), enzymatic ROS scavengers include different enzymes such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), ascorbate peroxidase (APX), dehydroascorbate reductase (DHAR),monodehydro ascorbate reductase (MDHAR) and glutathione reductase (GR). These antioxidants act as redox buffers along with ROS under stress condition and function as a metabolic interface which modulates the appropriate stimulation of acclimation/tolerance behaviour (Foyer and Noctor, 2005). Under the situation of stress, ROS behave as a token of signalling molecules to enhance the stress

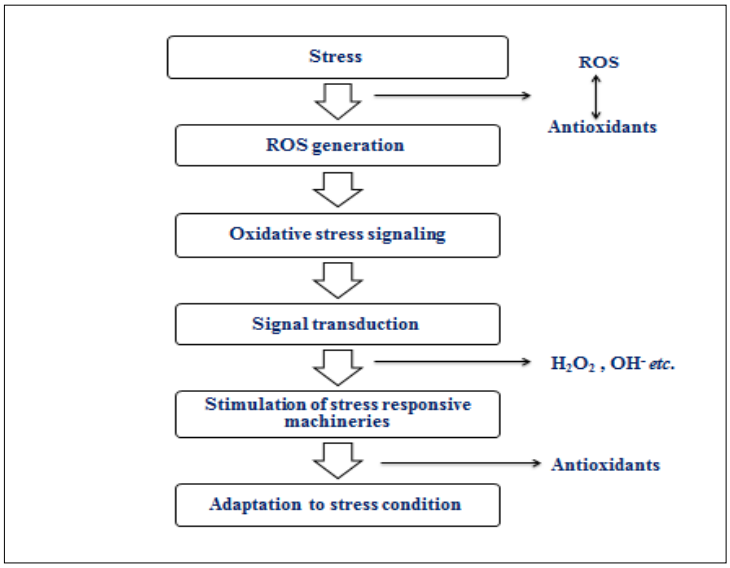

Fig 5: Adaptation of plant under stress condition.

responsive machineries which respond well against the stress (Fig 5). Ultimately, it can be said that these molecules activate and incentivize the acclimation/adaptation mechanism in plants (*Miller et al.*, 2010).

CONCLUSION

Based on the above discussion, it can be summarized that enhancement of tolerance to salinity in fruit crops would be an important target for plant breeders in order to ensure food supply for the growing world population. It is widely accepted fact that the genetic and physiological basis of salt tolerance in plants is inherently complex due to involvement of multigene regulated traits or mechanisms. Lack of thorough understanding of these mechanisms and their contribution toward salt tolerance is a major limitation in the development of salt tolerant plants. Additionally, the lack of proper screening methods, low heritability, inefficiency in the selection of competent traits and limited knowledge of interactions among the genotypes act as an obstacle in the breeding of salinity-tolerant crops. Genes responsible for different aspects of salt tolerance need to be identified, functionally characterized and transferred to commercially acceptable genetic backgrounds to develop new cultivars with enhanced salt tolerance. Although, in the past few decades, some progress has been made in the identification of genes, enzymes which play a significant role in salt tolerance and some transgenic “salt tolerant” plants have been developed, yet most of these plants had limited success for commercial utilization under saline field conditions Hence, for better understanding of the salt tolerant mechanism and bringing out new salt tolerant fruit crops/ rootstocks to cope up with saline environment, future research should be directed for the identification of molecules connecting pathways, the key components of each pathway and the characterization of individual genes and assessment of their contribution to salt stress tolerance, which will facilitate to engineer horticulturally important salt-tolerant fruit crop varieties and rootstocks.

Author’s contribution

P. K. Nimbolkar participated in compilation of literature of review, diagrammes and editing of article. Jyoti Bajeli participated in preparation of outline for writing manuscript, citation and writing review article. Arunima Tripathi participated in checking grammatical mistakes and cross check of whole article. Dr. A.K. Chaubey helped in writing manuscript and compilation of literature.

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