Strategies for Developing Salt Tolerant Rootstocks in Fruit Crops

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INTRODUCTION

Burgeoning global population has placed an unprecedented pressure on productive lands and fresh water. While prime farmlands have shrunk consistently (Ramankutty *et al*. 2002), global water resources continue to face the threats of salinization and pollution (Sharma and Singh, 2017), reducing their availability and quality to the extent that use of marginal quality water could be the only option for sustaining crop production in many areas across the world. With world population estimated to exceed 9 billion by 2050, an accompanying ~70% rise in global demand for food and feed is imminent (FAO, 2009). According to a recent estimate, sprawling urban centres alone could grab nearly 2.5% of the prime global lands in the next 10 years or so, slashing ~4% of the total global crop production compared to the 2000 level. In particular, many counties of Asia and Africa are likely to be hit severely due to rapidly depleting croplands (d'Amour *et al*. 2017). Irrigation sector is the single largest consumer of global fresh water. Estimates show that nearly 75% of the global water is currently being used in agricultural production while the remaining 25% is consumed by the industrial and municipal sectors. In some countries like India, irrigation accounts for a lion's share (~90%) of the total water consumption. By implication, substantial improvements in crop water use efficiency coupled with reduction in water wastages have become absolutely essential. An equal emphasis is also to be placed on tapping the non-conventional water resources in irrigation.

Despite an urgent need to augment the global crop harvests, yield gains even in staples like rice and wheat remain far below the desired levels (Ray *et al*. 2013). Of late, rising incomes, improved standards of living and the changing life styles, particularly in the developing countries, have also increased the demand for nutrient and calories rich food including fruits, vegetables, milk, egg and meat (FAO, 2009). Regardless of the commodity, consistently rising food demands can be met either by increasing the area under cultivation or by improving the current yield levels. However, both of these strategies have their own limitations. While further agricultural expansion into new areas is to be discouraged due to environmental concerns, crop intensification to boost the yields may cause irreparable damages to the natural resources. Evidently, extending the frontiers of agriculture to barren, unused and abandoned lands through the aid of improved technologies remains the only viable option to bridge the food supply gaps (FAO, 2011).

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Agricultural lands suffering from different climatic and soil-related constraints, both natural and anthropogenic, are collectively designated as ‘marginal lands’. Salt-affected soils (SAS), an important example of the marginal land, reduce crop productivity in about 1 Billion ha global area to varying extents. Presence of excessive amounts of soluble salts and/or exchangeable sodium causes a range of adverse impacts on soil properties and crop plants (FAO and ITPS, 2015). In this article, an effort has been made to show that development of high yielding salt tolerant cultivars should be the main priority to address the intertwined concerns of reduced water and amendment use and sustained fruit productivity in salt-affected soils.

Physico-chemical Properties of Saline Soils and Water

The values of soil saturation paste extract electrical conductivity (EC_e), pH (pH_s) and exchangeable sodium percentage (ESP) are used to categorize the soils into normal, saline, sodic and saline-sodic groups. In India, two categories of salt-affected soils are ‘saline’ ($EC_e \geq 4$ dS m^{-1}, $pH_s < 8.2$, ESP< 15) and ‘sodic’ ($EC_e < 4$ dS m^{-1}, $pH_s > 8.2$, ESP >15). Abundance of soluble salts, mainly consisting of the chlorides and sulphates of Na^+, Ca^{2+} and Mg^{2+}, raises the saturation extract electrical conductivity (EC_e) of soils (≥ 4 dS m^{-1}) which in turn leads to the reduced water availability and specific ion toxicities causing physiological abnormalities in plants. High exchangeable sodium percentage (ESP; >15) deteriorates the structure, impedes the water and air flows, reduces water intake capacity and hampers the root penetration in sodic soils. Current estimated area under SAS (6.74 M ha; comprising of 3.79 M ha sodic and 2.95 M ha saline area) is projected to increase to 16.2 M ha by 2050 (ICAR-CSSRI, 2015). In many salt-affected areas, groundwater is often also saline or sodic (alkali), imposing constraints on soil reclamation and further increasing the salt stress in crops. Salinity hazard of irrigation water can be determined by estimating the total dissolved salts, expressed as dS m^{-1} (EC), mg L^{-1} (ppm) or me L^{-1}. Similarly, sodium adsorption ratio (SAR), residual sodium carbonate (RSC) and adjusted SAR values are used to evaluate the sodicity hazard of irrigation water. Prolonged use of such waters often results in irreparable declines in soil quality especially in absence of suitable soil, water and crop management practices. In India, salty irrigation waters are classified into good ($EC_{iw} < 2$ dS m^{-1} and SAR < 10 mmol L^{-1}), saline ($EC_{iw} > 2$ and SAR < 10), high-SAR saline ($EC_{iw} > 4.0$ and SAR > 10) and alkali (EC_{iw} variable; SAR variable and RSC > 2.5 meq L^{-1}) categories.

Constraints Imposed by Irrigation-Induced Salinity

Salinity is a severe limitation to sustainable crop production in many areas of the top fruit producing countries like China (Li *et al*. 2014), India (Sharma and Singh, 2017), Brazil (Pessoa *et al*. 2016), United States (Anonymous, 2009) and Spain (Raya *et al*. 2004). Depending on whether salt-affected soils are formed due to natural or anthropogenic factors, agricultural salinity is categorized into 'primary' and 'secondary' groups, respectively. While primary salinity arising due to climatic and geological factors *viz*., extreme aridity, weathering of minerals, salt redistribution, etc. has long been an important yet somewhat manageable concern; the last few decades have seen relentless incresae in human-induced secondary salinization in both irrigated and dryland regions of the world. Depending on situation, irrigation-induced salinity (*i.e.*, secondary salinity) may refer to the formation of salt-affected soils *de novo* or to the further increase in soil salinity in areas irrigated with poor quality saline and sodic waters; especially when excess irrigation is done, drainage is neglected and the recommended salinity management prcatices are not implemented. In so far fruit crops are concerned, impacts of irrigation-induced salinity far outweigh than those of dryland salinity in terms of economic losses. This is because a large chunk of total global harvests in some of the most widely traded crops like citrus and grapes comes from the irrigated lands. Although some crops like date palm, olive and Indian jujube are adapted to dryland saline conditions and tolerate higher levels of salinity, they display marked reductions in fruit yield in absence of irrigation and also when continually irrigated with saline waters. Over the years, irrigation-induced salinity has increased considerably in the north-eastern semi-arid part of Brazil; an important fruit growing area (Pessoa *et al*. 2016). Salt buildup in the soils and groundwater is threatening the irrigated fruit production in the California valley of the United States with fine-textured alluvial soils underlain with a less permeable clay layer being especially vulnerable to salt-induced degradation (Schoups *et al*. 2005). Many coastal areas in the southeast Spain, where fruits like mango and avocado are commercially grown, are adversely affected by salinity to varying extents. The problem particularly becomes serious in dry years when seawater intrusion results in measurable reduction in fruit yields (Raya *et al*. 2004).

Irrigation-induced waterlogging and salinity problems have also emerged as serious constraints in many fruit growing areas of India. According to Bhargava *et al*. (2006) and (Mohan, 2015), irrigation water salinity has steadily increased in the semi-arid grape growing areas of Maharashtra and Karnataka states. In areas where EC_{IW} has exceeded 2.0 dS m^{-1}, use of salt excluder rootstocks along with other management practices would be inevitable to sustain vineyard productivity. In certain cases, even the use of suitable rootstocks may not be as effective as believed; a fact perhaps best illustrated by the breakdown of salt tolerance in the conventionally used ‘Dog Ridge’ rootstock. ‘Thompson Seedless’ vines grafted on ‘Dog Ridge’ and ‘Salt Creek’ do not withstand continual exposure to saline irrigation (≤6.5 dS m^{-1}) compared to those on ‘B2-56’ and ‘1613C’ with the latter two being effective in maintaining a lower Na^+: K^+ ratio and thus lesser injury to the shoot system (Sharma *et al*., 2011). Adverse growing conditions, *viz.*, high salinity, drought and heat stress are the major limitations to ‘Kesar’ mango cultivation in the Saurashtra region of Gujarat. Use of salt tolerant rootstocks is being explored to tide over the salinity problem (Balan, 2017). Consistently rising saline watertables have brought the once thriving Kinnow mandarin industry in south-western region of Punjab to standstill. Extent of the problem is evidenced by the fact that unabated salinity has led to the sudden collapse of Kinnow orchards village after village. The problem in part can be explained by the replacement of Cleopatra with rough lemon in budding. Earlier, Kinnow growers used the scions budded on Cleopatra mandarin- one of the best salt excluder rootstocks. However, in the last two decades or so, cost and other considerations have led to widespread use of plants budded on rough lemon- a salt sensitive rootstock. A more or less situation prevails in the south-western parts of Haryana where Indian jujube was a predominant fruit grown until recently. Farmers facing the twin menaces are increasingly switching over to other land use option, including the non-conventional rice crop in some of the critically affected pockets. Of late, irrigation-induced sodification in canal commands and the resodification of reclaimed soils is slowly emerging as a major soil constraint in the central Indo-Gangetic plains where mango is the main commercial crop (ICAR-CSSRI, 2017).

Physiological Basis of Salt Tolerance

Similar to other crops, fruit crops exhibit different physiological and molecular adaptations to cope up with excess salts in soil and irrigation water. Different such mechanisms employed to prevent salt entry into plants may be operative either at the molecular or cellular or whole plant levels. Both salt tolerant halophytes and salt sensitive glycophytes tend to achieve salt tolerance by the selective ion uptake, preferential loading of K^+ into xylem and retention of Na^+ in the basal stem and root tissues (Munns *et al*., 2002). However, these responses are essentially genotype-specific implying that a set of mechanisms function in a particular genotype may not be present in others. Given the fact that plants transpire 30-70 times more water than they use for cell growth, salt exclusion assumes great significance to prevent the excessive tissue concentrations of salts carried along the transpiration stream. In non-excluder or poorly salt-excluder genotypes, foliage salt concentrations may shortly attain damaging levels (Munns, 2002). Salt exclusion is especially desirable in perennial fruit crops retaining the leaves for much longer periods than annual field crops. In perennial species, morphological and anatomical features like high shoot: root ratio, high intrinsic growth rates and absence of apoplastic pathway in roots decrease salt loading into the transpiration stream. Furthermore, in relatively more salt tolerant species, minimal retranslocation of absorbed salt ions (Na^+ or Cl^-) in the phloem would prevent the salt accumulation in the actively growing shoots and leaves.

At the cellular (organelle) level, salts present in the cytoplasm are sequestered into cell vacuole (i.e., ion compartmentation) to prevent damage to the cytoplasmic enzymes. At concentrations above 100 mM, both Na^+ and Cl^- inhibit the enzymatic activities. Subsequent to the sequestration of Na^+ and Cl^- in the cell vacuole, a range of inorganic and organic solutes accumulate in the cytoplasm (*i.e*., osmotic adjustment) to balance the osmotic pressure of the ions in the vacuole. In comparison to salt exclusion, ion compartmentation and osmotic adjustment entail higher energy use to synthesize the solutes. Again, accumulation of compatible organic solutes requires much more energy compared to that needed for inorganic ions (*i.e*., 3.5, 34, 41 and 50 moles of ATP for Na^+, mannitol, proline and glycine betaine, respectively; Munns, 2002). At the molecular level, different ion channels and transporters regulate the net movement of salts across the cell membranes. As hydrated ionic radii of Na^+ and K^+ are strongly similar with each other, ion channels often fail to discriminate between them. Na^+ ions can be transported into the cell through low- and high-affinity K^+ transporters (Blumwald, 2000). Low-affinity K^+ channels with low K^+/Na^+ selectivity are more adversely affected by Na^+ ions.

Naturally, salt treated plants need to maintain high-affinity K^+ channels for adequate K^+ uptake (Zhu, 2007). Three types of low affinity K^+ channels including inward rectifying channels (KIRCs), outward rectifying channels (KORCs) and voltage-independent cation channels (VICs) are found in plants. In contrast to voltage dependent KIRCs and KORCs having a high K^+/Na^+ selectivity ratio at physiological K^+ and Na^+ concentrations, VICs exhibit a relatively high Na^+/K^+ selectivity and are implicated in Na^+ uptake at high salt levels (Blumwald, 2000). Integrated membrane proteins (IMPs) present in plasma membranes play a crucial role in different cell functions including control of the solute movement across the membranes. High-affinity potassium transporters (HKTs) are a class of IMPs occurring only in plants. While some HKT proteins are highly selective for Na^+, others exhibit affinity for K^+. Moreover, the selectivity of certain HKT proteins may change depending on the ionic environment (Waters *et al.*, 2013). While Cl^- may prove much more injurious than Na^+ in many species, little is known about Cl^- uptake and translocation mechanisms in plants. Some of the key traits that control Cl^- transport processes in plants include reduced net xylem loading, intracellular compartmentation and efflux of Cl^- from roots. Restricted loading into xylem prevents excess Cl^- accumulation in the shoot tissues. Recent observations suggest that genes and proteins directly or indirectly regulating Cl^- flux in plants include the aquaporins (regulating the water flow in roots) and ATP binding cassette (ABC) transporters. Transcriptome analysis of two citrus genotypes differing in Cl^- exclusion revealed the possible involvement of several anion transporter families (Teakle and Tyerman, 2010).

Measures to Improve Salt Tolerance

Fruit growers can harness different options to mitigate salt stress in the orchards. First and foremost, efforts should be made to select the lands having moderate salinity and deeper watertables as majority of the fruit crops are highly vulnerable to high salinity and waterlogging in the root zone. In areas where watertable lies below 2 m from the land surface, and preferably at 4-5 m depth, the chances of direct contact between tree roots and saline water will be minimal. Plants suffer from severe salt stress when the watertable is <1.5 m below the soil surface because shallow watertables not only hinder salt leaching but also induce upward flux of the salts present in water. In lands where watertable lies at 1.5-3.0 m depth, evaporation induced salt accumulation on the surface will be minimal (Salama *et al.*, 1999). In waterlogging free sodic lands with adequate supply of fresh water, treatment of planting pits with amendments like FYM, sand and gypsum may alone give good results. Other agronomic options for reducing salt stress in fruit crops include mulching with inorganic and organic materials, planting on raised beds, precautions in nutrient management and drip irrigation. However, some of these practices may often be cost prohibitive and may involve recurring expenses, stalling their widespread use. Regardless of the depth of watertable (shallow or deep), use of salt tolerant cultivars is always desirable to lessen the dependence on such means of salinity management; albeit with caution because sole dependence on a single practice (*e.g.*, rootstock) may not be sustainable in the longrun. This suggests the need for integrated use of doable salinity management techniques in fruit crops.

Development of Salt Tolerant Rootstocks

A salt tolerant rootstock may be defined as the one which excludes a considerable portion of salts from roots without any adverse effects on water and nutrient absorption. Additionally, many salt tolerant rootstocks may modulate responses of the scion cultivar(s) in ways that greatly reduce the harmful effects of salt ions after their entry inside the plant. Either complete or partial salt exclusion would prevent the shoot salt concentrations from reaching toxic levels, allowing the normal plant metabolism. Development of salt tolerant rootstocks can be achieved either by identifying the natural variations through direct selection, by hybridization, induced mutagenesis or by using various biotechnological methods. Limited success in rootstock selection trials under field conditions can be attributed to the influence of environmental factors on whole plant response. Again, convincing evidence is currently lacking as to which component(s) of intricate physiological network contribute considerably to improve the overall performance of a crop genotype at a particular growth stage even in the widely studied crops like citrus; rendering physiological criteria somewhat less effective for selection. Consequently, interest has increased in identifying and characterizing the genes and their products for introgression into popular yet salt sensitive cultivars via marker-assisted breeding and genetic transformation.

Exploiting Natural Variations through Selection and Hybridization

Despite substantial efforts in the last few decades, commercial release of salt tolerant cultivars through selection and hybridization in general has been rather slow, which is attributable to the complex inheritance of salt tolerance and the problem of linkage drag in the conventional methods of improvement. Slow progress in this direction has spurred the interest in alternative means; development of easily propagable, salt tolerant rootstocks being one of them. Use of salt tolerant rootstocks for managing salinity and other stresses is even being encouraged in vegetable crops multiplied commonly through seeds. The interest in salt tolerant rootstocks emanates from the fact that their use in grafting could safeguard the actively photosynthesizing leaves and shoots from salt injury. In addition to reduced salt translocation to the foliage, grafted plants may also be used as genetic models to understand the influence of genes transcribed in the roots on shoot growth.

Most of the fruit crops, even those considered to be highly salt sensitive (e.g., citrus and mango), exhibit considerable genetic variation for salt tolerance. Even crops ranked as moderately salt tolerant (e.g., olive) display considerable inter-cultivar differences in salt tolerance. Hoult *et al*. (1997) screened 21 polyembryonic mango rootstocks of which Orange, Golden Tropic, Banana, Red Haruman, and Pico exhibited good salt exclusion capacity when exposed to NaCl (480 ppm) salinity. However, none of the tested rootstock was efficient in excluding both Na^+ and Cl^-. The extent of leaf marginal scorch also varied between cultivars.

Similarly, Marin *et al*. (1995) found that salt treated (100 mM NaCl) olive cultivars differed widely with each other after 49 days of salt treatment. In comparison to 60-70% relative growth compared to control in the tolerant cultivars (Nevadillo, Jabaluna, Escarabajuelo, Caiiivano and Picual), relative growth was below 30% that of control in the sensitive cultivars (Pajarero, Chetoui, Galego and Meski).

These observations imply the need for screening the maximum possible number of genotypes *viz*., released cultivars, genetic stocks and wild relatives to reach to meaningful conclusion regarding the salt tolerance threshold in a given fruit crop. Again, actual salt composition of soil and groundwater of a particular area must be taken into account to avoid the erroneous interpretation of results. This is because differences in the salt composition of experimental soils and waters with that of areas being targeted for fruit cultivation may not lead to expected results. Ironically, researchers seldom take this consideration into account and use either a single salt (NaCl) or salt mixtures that poorly match with those of salt-affected lands (Grieve et al. 2012). Thus, in order to avoid biased interpretations, screening experiments should be carried out using the local salty soils and waters. However, resource, time and space constraints may not always allow the evaluation of a large germplasm collection under such ideal conditions. When field trials are not possible for one reason or other, controlled experiments in pots, lysimeters etc. may be conducted using methods and procedures that could create an environment closely similar to field conditions. In addition, the results of such controlled studies must be verified by long-term field trials to draw valid conclusions. Salt tolerant rootstocks identified using such relatively controlled experiments are given in Table 1.

Table 1: Salt tolerant rootstocks identified in different fruit crops

Crop	**Rootstock(s)**	**Reference**
Citrus	‘Cleopatra’, ‘Gou Tou Cheng’	Levy *et al*. (1999)
	‘Rangpur lime’	Storey (1995)
Guava	‘Crioula’	Sá *et al*. (2016)
Grape	‘Dogridge’, ‘Salt Creek’ (syn. ‘Ramsey’)	Upreti and Murti (2010)
	V. berlandieri × *V. rupestris* (110R, 1103P, 99R, B2/56)	Jogaiah *et al*. (2014)
	‘1103 Paulsen’	Walker *et al*. (2004)
Indian jujube	*Z. rotundifolia*	Gupta *et al*. (2002)
	Z. nummularia	Meena *et al*. (2003)
	Z. spina-christi	Sohail *et al*. (2009)
Mango	‘13-1’	Kadman *et al*. (1976)
	‘Gomera-1’	Duran *et al*. (2003)
	M. zeylanica	Schmutz (2000)
	‘GPL-1’ and ‘ML-2’	Damodaran *et al*. (2013)
	‘Olour’, ‘Nekkare’	Pandey *et al*. (2014)
Prunus spp.	‘GF$_{677}$’	Massai *et al*. (2004)
	‘Myrobalan’, ‘Bright’s Hybrid’	El-Motaium *et al*. (1994)
Pear	*Pyrus betulifolia*	Okubo and Sakuratani (2000)
Pistachio	*P. atlantica*, `UCB-1'	Ferguson *et al*. (2002)
Pomegranate	‘Tab-o-Larz’	Karimi and Hassanpour (2017)

Selection for Unique Traits

Certain morphological and genetic factors like root traits, polyembryony and polyploidy may also greatly modulate the salt tolerance with individuals showing a particular character likely to be more salt tolerant. However, information on these aspects is scanty in most of the fruit crops. Some authors have studied the effects of root morphology on salt tolerance in citrus and olive. According to Rewald *et al*. (2012), 'root order'- the position of individual root segments in the root branching hierarchy- can have a strong influence on plant adaptation under stress conditions. In order to verify this hypothesis, they studied the phenological and physiological plasticity in the root orders of salt stressed *Citrus volkameriana* rootstock. Chloride accumulation significantly increased with decreasing root order, and the Cl^{-} concentration in lower root orders exceeded that of leaves. While water flux densities of higher root orders changed marginally, those in second- and third-root orders increased by 2- to 6-fold after short-term stress release. Changes in root order frequency, morphology, and anatomy indicated rapid and major modifications in *C. volkameriana* root system under salt stress. Rewald *et al*. (2011) examined the long-term effects of salinity on water uptake and root carbon assimilation in two olive varieties, *viz*., Barnea (tolerant) and Proline (sensitive). The trees were irrigated using normal (1.2 dS m^{-1}) and saline [4.2 (both varieties) and 7.5 dS m^{-1} (Barnea only)] waters for 11 years. Although both varieties exhibited reduced fine root biomass under salinity, 'Proline' showed a smaller fine root system than 'Barnea', and thus a higher root sap-flow density in 'Barnea'. 'Proline' trees also had a lower root biomass: necromass ratio than 'Barnea'. Fine root system reduced the deleterious effects of salinity by influencing slat exclusion, water uptake and carbon allocation. Tozlu *et al*., (2000) studied the effects of salinity (0, 30, 60, 90, and 120 mM NaCl) on *Poncirus trifoliata* cv. Pomeroy. They observed that continuous production of fine roots, a trait called 'fine root turn over' helped the plants in removing the excess ions and thus delaying the onset of ion accumulation in root tissues. Plants were also able to delay the accumulation of Na^{+} but not Cl^{-} ions in leaves as evidenced by high levels of Cl^{-} in the leaves and of both the ions in fine roots. This phenomenon, unique to *P. trifoliata*, seems to be transferable to other citrus species through inter-generic hybridization.

Fruit crops like citrus, mango, bael and jamun exhibit polyembryony. Polyembryonic seeds contain a single zygotic embryo and many nucellar embryos arising from the diploid maternal tissue. Although nucellar embryony is a bane for citrus hybridization resulting in the poor or no survival of sexual seedlings, it could be a boon for propagation: highly nucellar types mostly produce true-to-type seedlings (Moore and Castle, 1988). The existing diversity of polyembryonic types in these crops needs to be harnessed for developing true-to-type and easily multipliable salt tolerant rootstocks. Several authors have reported that polyembryonic mango seedlings often do well under saline conditions (Bright *et al*., 2001; Hoult *et al*. 1997; Pandey et al. 2014). One plausible reason for higher salt tolerance in polyembryonic mangoes seems to be their natural adaptability to salt-rich environments. Most of the currently known polyembryonic mangoes are believed to have originated in the coastal areas where periodical inundation of seawater frequently occurs. Despite convincing evidence regarding the usefulness of polyembryonic rootstocks in alleviating the salt stress, commercial mango cultivars in India continue to be grafted on non-descript monoembryonic seedlings. In certain crops, salt tolerance of individual genotypes may vary with their ploidy level. In citrus, for example, tetraploid seedlings may display higher salt tolerance than diploid ones. It is believed that genome duplication can modify certain anatomical and physiological traits, enhancing the efficiency for salt exclusion. Diploid *Citrus macrophylla* seedlings absorbed more Na^+ and Cl^- in leaves than tetraploids under two NaCl levels (40 and 80 mM). Leaf K^+ concentrations declined only in the diploid seedlings reflecting the differences in mineral uptake and translocation (Ruiz *et al*., 2016).

Shortening the Breeding Cycle

As previously shown, fast genetic improvement of perennial tree fruits is often constrained by the extended breeding cycles such that development of new cultivars may take 2-3 decades to materialize. Based on a review of literature, van Nocker and Gardiner (2014) found that several agronomic, biotechnological and genomic options are available for reducing the breeding in tree fruits. Agronomic manipulations essentially aim to create an optimum environment for the plant growth by lessening the impacts of different biotic and abiotic stresses. Under optimal conditions, apple seedlings may produce flowers as early as 10 months after transplanting in contrast to the field grown seedlings which come into flowering after 4-5 years. Exogenous applications of certain plant growth substances may also be helpful in some crops. Embryo rescue technique can be used for dissecting the embryos followed by their culture on suitable media for reducing the weeks of chilling requirement in many temperate fruits. Biotechnological techniques, especially genetic transformation, can also be a potential solution for reducing the length of breeding cycle. Beginning with '*LEAFY*' genes from *Arabidopsis*, there have been several successful attempts for manipulating the endogenous flowering pathways by deploying the flowering genes with the aid of inducible promoters.

Use of Molecular Techniques

Although voluminous literature is available on various physiological and biochemical traits underpinning salt tolerance in crop plants, development of salt tolerant cultivars has met with little success. This situation can be ascribed to the fact that genetic improvement for salt tolerance has received little attention of plant breeders in most of the countries with almost exclusive focus on increasing crop yields and quality under normal soil conditions. However, commercial release of several salt tolerant cultivars in crops like rice, wheat and mustard in countries like India supports the conviction that genetic improvement for salt tolerance is not difficult to achieve. Limited success in the development of salt tolerant fruit cultivars can partly be explained by the low genetic variation in some crops, poor understanding of the genetic basis of salt tolerance in most of the species, and the problems encountered in the field experiments. Precise genetic basis of salt tolerance remains debatable even in the most studied crops like grapevine with some researchers considering it to be 'monogenic' while others treating it a 'polygenic' trait (Gong et al. 2010). Large-scale field and laboratory studies for deciphering the genetic regulation are tedious and costly. Again, if adequate resources are available, correct predictions of absolute salt tolerance under field conditions may not always be possible; there are intricate, often undetectable, interactions between the environmental stimuli and trait expression. This has prompted many investigators to study plant response to salts under relatively controlled (pot) experiments, but to little avail. Because plants exhibit a suit of physiological mechanisms to blunt the adverse effects of excess salts, pot experiment results poorly correspond with the field observations.

In vitro Screening

Some authors consider *in vitro* culture studies to be a more economical and precise way of elucidating the physiological and molecular basis of salt tolerance. Erturk *et al.* (2007) studied the *in vitro* response of sweet cherry rootstock Gisela 5 (*Prunus cerasus* × *Prunus canescens*) to increasing NaCl levels (0-150 mM) *in vitro*. While salinity reduced growth and chlorophyll content, there was no effect on water content. Increased malondialdehyde content suggested salt-induced oxidative stress in shoots. Antioxidant defence system was activated; shoot Na^+ levels increased, K^+, Ca^{2+} and Mg^{2+} nutrition was impaired but shoot Cl^- was not affected. Similarly, Tewary et al. (2000) screened five mulberry genotypes (G2, G3, G4, S13 and S34) under salt and osmotic stress conditions. They observed that genotype G4 outperformed others in terms of sprouting percentage and shoot length up to NaCl concentration of 1.0% and pH 9.5. However, S13 exhibited the highest sprouting percentage and shoot growth compared to the other genotypes under osmotic stress. Despite such observations, results of *in vitro* experiments often do not confirm to the findings *in vivo*, implying the need for further refinements for making this technique more acceptable for routine studies.

DNA-based Markers, QTL and Association Mapping

Molecular markers like RAPD, AFLP, SSRs and recently SNPs have been successfully applied for estimating the genetic diversity, generating unique fingerprints for varietal identification, testing the progeny purity and for other purposes in fruit crops. Application of randomly amplified polymorphic DNA (RAPD) markers showed that certain DNA fragments were probably linked to genes coding for salt tolerance in date palm (Kurup et al. 2009). DNA-based markers have also been used to map the quantitative trait loci (QTLs)- the genomic stretches regulating the variation of a quantitative trait of interest like salt tolerance arising due to combined action of multiple segregating genes and the environmental stimuli. In QTL analysis, two parents divergent in one or more quantitative traits, are crossed and the resulting hybrid progeny is analyzed to identify the DNA marker(s) linked to a particular trait for indirect selection. In tomato, QTL analysis showed that salt tolerance was a heritable trait influenced by at least eight medium sized QTLs inherited from the wild parents (Estañ et al. 2009). Similarly, 98 QTLs were found to be putatively associated with salt tolerance in a hybrid citrus population derived from Cleopatra mandarin (salt tolerant) x Trifoliate orange (salt sensitive) cross. (Raga et al. 2016). QTL mapping also indicated that nearly 70% of the six dozen QTLs were putatively associated with salt stress regulation in a back cross citrus population [*Citrus grandis* x (*Citrus grandis* x *Poncirus trifoliata*)] (Tozlu et al. 1999). It has also been shown that QTLs linked to salt tolerance in citrus may also regulate the tolerance to other abiotic factors like cold stress (Moore et al. 2000). However, one important demerit of QTL mapping approach is that it cannot reveal the role of allelic variations in the whole gene pool in modulating the trait expression (Long et al. 2013). This has led to a gradual shift towards other potential techniques like association mapping (AM) made possible by rapid advances in genotyping, genome sequencing and statistical analysis. Association mapping, also referred to as linkage disequilibrium (LD) mapping, seeks to unravel the intricate variations in a particular trait by investigating the evolutionary recombination events at the population level. In contrast to QTL mapping limited to exploring the variations between two contrasting individuals, AM permits the survey of phenotypic and genetic differences across population (García-Lor et al. 2012; Zhu et al. 2008). In the recent years, whole genome sequences have become available in crops like apple, peach, grapes, papaya and strawberry while sequencing work is in progress in other fruit crops. Availability of cost efficient high-throughput techniques may further accelerate sequencing and genotyping studies, eventually leading to their use for identifying more efficient markers like single nucleotide polymorphisms.

Structural and Functional Genomics

Availability of complete DNA sequences in many crops is allowing the researchers to determine the gene functions by studying the number and structure of genes in a particular genome (Pichersky and Gerats, 2011). A little over half of the plant genes known can be assigned some kind of function by comparing them with the genes sequences having known function. However, an understanding of the general function of a gene will not be sufficient to understand its specific role and thus functional genomics studies have become necessary to assign particular functions to such genes (Somerville and Somerville, 1999). On the basis of sequencing information, gene function can be predicted either by ‘forward’ or ‘reverse’ genetics approaches. However, considering the fact that forward genetics is by and large unsuitable for high-throughput functional analyses, use of reverse genetics approach is preferred. In this approach, a specific nucleotide sequence is used to establish the association between nucleotide sequence and the underlying function(s) by studying mutations that disrupt the sequence (Peters et al. 2003).

High-throughput Techniques

It is increasingly being realized that advent of the so-called ‘omics approaches’ would greatly accelerate the speed and accuracy of the functional genomics. These efficient high-throughput omics tools including transcriptomics, proteomics and metabolomics have been defined as the ‘global (genome-wide or system-wide) experimental approaches to assess the gene function' (Bouchez and Höfte, 1998). Transcriptome refers to the complete set of cell- or tissue-specific messenger RNA (mRNA) molecules expressed by an organism. In contrast to plant genome, transcriptome expression depends on particular growth stage and the environmental conditions, and such changes in expression can be measured by using appropriate techniques. Innovations in inexpensive high-throughput next-generation sequencing have increased the efficiency of transcriptome sequencing for studying the global transcriptional networks. One study showed that expression of genes involved in polyamine biosynthesis was modulated by salt treatment (NaCl) in sour orange (*Citrus aurantium* L.) (Tanou et al. 2014). Differential expression of about 1900 genes involved in protein biosynthesis and signaling pathways in the roots of mock- and salt-treated date palm plants indicated their putative functional roles in salt tolerance (Radwan et al. 2015). Salt treatment induced the expression of about 2600 genes in leaves and nearly 4700 genes in roots in date palm cv. Khalas. Of these, 194 genes were commonly expressed in both the organs (Yaish et al. 2017). Differentially expressed mRNA and miRNA have been found to be involved in ABA-activated signaling pathway and ROS metabolism under dehydration and/or salt stress in *Citrus junos* cv. Ziyang roots (Xie et al. 2017). In Cabernet Sauvignon vines, salinity stress triggered higher number of transcripts involved in protein synthesis and metabolism (Cramer, 2007). Salt tolerant grape genotypes (H6 and Gharashani) differed with salt sensitive (Shirazi and GhezelUzum) ones in gene expression under salinity with VvChS and VvPAL transcripts significantly increasing only in the leaves of tolerant genotypes (Mohammadkhani et al. 2016). Salt tolerant olive cv. Kalamon expressed a total of 209 transcripts compared to only 36 transcripts in salt sensitive cv. Chondrolia Chalkidikis upon salt treatment. Surprisingly, all the transcripts were downregulated in Kalamon after salt stress was relieved (Bazakos et al. 2012).

Along with the changes in transcriptome, abiotic stresses like salinity also elicit the changes in plant proteome and metabolome. It is worth to mention, however, that changes in gene expression do not necessarily lead to the changes in protein expression making it necessary to study the proteomic changes such that proteins directly influencing plant stress response may be identified. Proteome analysis, by dissecting the complete set of proteins, helps in understanding the different roles of proteins in stress regulation. A total of 85 leaf proteins showed quantitative variations in salt treated *Citrus aurantium* L. plants, but not in plants pre-treated with H_2O_2 or sodium nitroprusside (SNP). An overlap between H_2O_2 and NO signaling pathways in plant adaptation to salinity was also observed (Tanou et al. 2009). In salt stressed sour orange plants, a total of 271 S-nitrosylated proteins commonly or individually affected by salinity and polyamines were identified (Tanou et al. 2014). While 35 protein spots were seen in salt treated date palm plants, polyethylene glycol induced drought stress produced only 9 spots (El Rabey et al. 2016). Proteins involved in photosynthetic assimilation and protein synthesis declined in salt and water stressed Chardonnay and Cabernet Sauvignon grapevines. While most of the proteins upregulated in tolerant cultivar Chardonnay were of an unknown function, those in Cabernet Sauvignon were involved in protein metabolism (Vincent et al. 2007).

Although ground breaking advances have been made in transcriptome and proteome analysis, precise gene function(s) still remain obscure. In metabolomics, diverse metabolites produced by the plants are analyzed using high-throughput techniques. However, it is a cost prohibitive technique and may also entail very rigid technical procedures (Hall et al. 2002). Advocates of metabolomics approach believe that biochemical response of an organism to an environmental stress can be precisely elucidated by investigating the accumulation patterns of different metabolites. Like other crops, a suit of metabolites involved in the osmotic adjustment, anti-oxidant defense system and chlorophyll biosynthesis play a critical role in adaptation of fruit plants to salt stress. However, compared to other crop groups, little is known about the function of complete metabolite network in salt stress regulation in fruit crops. Water stressed Cabernet Sauvignon grapevines displayed higher concentrations of glucose, malate, and proline than salt treated vines (Cramer et al. 2007).

Genetic Transformation

Genetic improvement for yield and quality in general, and for stress tolerance in particular using conventional methods is resource intensive and cumbersome in perennial fruit trees. Extended juvenile period, gigantic tree size and the need for evaluating a large number of seedlings are some of the major factors hampering the success of tree breeding programs. Contrarily, incorporation of genes through *Agrobacterium*-mediated or other direct transfer methods like electroporation may substantially lower the time and costs with traditional selection and hybridization programs. Taking a cue from the successful application of transgenic technology in hundreds of plant species coupled with the availability of genetically modified food products on the market, fruit breeding programs across the globe are increasingly tapping genetic transformation technology for the breeding more productive and stress resilient fruit cultivars. However, many biological, regulatory and social constraints will have to be adequately dealt with to facilitate commercial applications of this technology in fruit crops. Transgenic *Arabidopsis thaliana* plants over-expressing the chemically synthesized grape gene *VvbHLH1* endured salt and drought stresses; an effect attributed to the upregulation of the genes involved in flavonoid and proline biosynthesis, ABA signaling pathway and ROS (reactive oxygen species) removal (Wang et al. 2016). Introgression of *Arabidopsis* vacuolar Na^+/H^+ antiporter gene (AtNHX1) improved osmotic adjustment and antioxidant activities in kiwifruit plants to the extent that they could tolerate up to 200 m mol l^{-1} NaCl (Tian et al. 2011). Salt treated transgenic banana lines over-expressing *MusaDHN1* gene showed higher proline accumulation and decreased lipid peroxidation compared to wild type plants (Shekhawat et al. 2011). Recently, transgrafting has also emerged as a potentially novel technique to alleviate some of the fears related to transgenic technology. In transgrafting, either genetically engineered scion or rootstock having potential to confer tolerance to stress conditions is used as one of the graft components (Haroldsen et al. 2012).

Conclusions

Global salt-affected area is projected to increase substantially in the foreseeable future due to fresh water scarcity, irrigation management, rampant use of poor quality waters in irrigation and the climate change impacts. Ironically, soil reclamation through conventional means is increasingly becoming difficult. In the face of the rising amendment costs and rapidly depleting fresh water, there is a tangible shift from mitigation to adaptation measures for salinity management. Use of salt tolerant plants is suggested as an affordable and efficient approach to obtain stable harvests under saline conditions, with reduced or no use of fresh water and amendments. In fruit crops, development of salt tolerant scion cultivars is cumbersome and cost prohibitive shifting the emphasis on developing salt excluder rootstocks. Reduced uptake of salts by the roots can considerably lessen injurious effects on the fruit bearing shoot system. Rootstocks capable of either fully or partially excluding Na^+ and Cl^- ions and exerting other beneficial effects on the shoot system have been identified in many fruit crops. However, less than potential use in many cases and the decline in salt exclusion capacity upon prolonged exposure to salinity in some others have necessitated the reliance on biotechnological approaches to develop the rootstocks compatible with the location-specific needs. In many situations, rootstocks having tolerance to multiple stresses may be desirable. Breakthroughs in the fields of molecular marker-assisted breeding, genomics, omics technologies and genetic modification are greatly aiding to the efforts of fruit breeders and physiologists in understanding the complex biochemical and molecular networks imparting salt tolerance to fruit crops. Recent advancements have made these technologies economically affordable resulting in their increased use for accelerating the fruit crop improvement. The observations presented in this article make it evident that day is not far off when these technologies will open a new frontier in the development of salt tolerant rootstocks capable of enduring the excessive levels of salinity and associated problems currently unachievable through conventional means.

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