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Morphological, Physiological, Biochemical and Molecular Facet of Drought Stress in Horticultural Crops

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Abstract

Water stress disrupts horticultural crop growth, development and finally results in low productivity particularly in arid and semi arid parts of the world. Plants require certain physical, chemical and biological factors for their growth and development. Any deviation from these factors may cause aberrant metabolic changes and plant experience a tension known as stress. Water stresses trigger a wide variety of plant responses, ranging from altered gene expression and cellular metabolism to changes in plant growth, leaf morphology and movement and root development and finally productivity. Drought stress modifies photosynthetic rate, relative water content, leaf water potential, and stomatal conductance. Finally, it destabilizes membrane structure and permeability, protein structure and function, leading to cell death. Drought tolerant plants possess various mechanisms like reduction in water loss by reducing stomatal conductance or morphological modification, improving water uptake by developing efficient root systems and accumulation of osmolytes. Management practices employed for drought stress management in horticultural crops include use of drought tolerant crop varieties, use of tolerant root stocks, canopy management, wind breaks, regulated deficit irrigation and partial root zone drying, uses of anti-transpirants etc. The varieties selected should have deep root system (bael, ber), leaf shedding (ber, lasoda, pomegranate), thorns on stem (ker, karonda, ber), stomata at lower side (custard apple), wax coating (ber), thin foliage and leaf orientation (aonla), hair on leaf and sunken stomata (fig, phalsa, ber and lasoda). This paper elaborates physiological, biochemical and molecular mechanism of drought tolerance along with drought stress management in horticultural crops.

Keywords: Drought stress, morphological modifications, stomatal conductance, osmolytes

1. Introduction

Horticultural plants require certain physical, chemical and biological factors for their growth, development and economic production. Any deviation from these factors may cause aberrant metabolic changes in plant which reduce crop yield. Plant stresses are broadly classified into two categories i.e. abiotic and biotic stress. Abiotic stress includes physical (water deficit, flooding, temperature, radiation, mechanical, electrical and magnetic etc.) and chemical (air pollution, allelochemicals, nutrients, pesticides, toxins, salts, pH of solution) factors while biotic factors are insect, pest, disease, microbes, competition between plants, allelopathy, lack of symbiosis and human activities. These factors cause imbalance in the natural status of environment that alter normal

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equilibrium and which leads to a succession of morphological, physiological, biochemical and molecular changes in plants, which unfavorably affect their growth, development and potential yield. Conversely, plants develop innate adaptations to these stress conditions with a wide range of biochemical and physiological interventions that involves the function of many genes in stress (Lisar et al., 2012).

Abiotic stress causes changes in the soil-plant atmosphere continuum (SPAC) and can lead to reduced yields and decreased plant performance. These stresses are sensed in the plant and plants can either respond by increasing their tolerance or avoidance through morphological modification and/or physiological, biochemical and molecular mechanism. These strategies lead to physiological and developmental changes that affect the productivity and growth of the tree. In horticultural crops, unfavorable conditions of these abiotic and biotic factors adversely affects the plant growth, development and interfere with complete expression of genotype potential yield. It is estimated that only 9% area of world is conducive for crop production while 91% is under stress. Abiotic stresses cause 71% yield reduction (Ashraf et al., 2008) and mostly crops are only reaching 20% of their genetic potential. The most significant abiotic stress is water stress, both deficit stress (drought) and excess stress (flood). The estimation of potential yield losses by individual abiotic stresses are 17% for drought, 20% for salinity, 40% for high temperature, 15% for low temperature and 8% for other factors (Ashraf and Harris, 2005). Plants experience water stress either when the water supply to their roots becomes limiting or when the transpiration exceeds absorption rate. Water stress reduces plant water potential and wall pressure to the extent that plant faces difficulty in executing normal physiological activities. Water stress is mainly caused by the water deficit, i.e. drought or high salt concentrations. In case of salt concentrations, water logging and low soil temperature, water exists in soil solution but plants unable to uptake it, this situation is known as physiological drought. Drought occurs frequently in arid and semi-arid climates with uneven precipitation. Drought refers to lack of precipitation over prolonged period of time where any area receive s annual rainfall less than average rainfall while water logging is a condition where water is present in excess amount than its optimum requirement which creates anaerobic condition around roots and plant unable to absorb water.

The irrigated area in the country has been increased from 22.6 M ha in 1950-51 to 88.4 M ha in 2009-10 and the contribution of irrigated agriculture is more than two-third to overall food production. It is predicted that by 2050, agricultural sector would require additional 45% water whereas its share is expected to decline by 10%. About 58% (80 M ha) of the net sown area in India continues to be rainfed that contributes 40% of the food grain production and supports two-third of the livestock population (Anonymous, 2015). During stress fruit TSS, titrable acidity, firmness, colour, ascorbic acid,

anthocyanins, phenols, flavonoids and post harvest desirable quality were increased in kiwi, strawberry, apricot, pear, grape and tomato etc. (Nora et al., 2012).

2. Water Stress and Horticultural Production

Every year, water stress particularly drought hamper horticultural crop growth, development and finally results in low productivity. Hence, the ability of horticultural plants to tolerate stress has immense economic importance. In India during 2013-14 horticultural crops contributed 277.40 million MT in production from an area of 24.20 million hectare with 11.50 MT ha⁻¹ productivity. Out of which fruit crops production was 88.97 million MT from 7.21 million hectare area and 12.30 MT ha⁻¹ productivity while vegetables share was 162.89 million MT from 9.39 million hectare area and 17.30 MT ha⁻¹ productivity (NHB Database, 2014). In world, India ranks number two after China in fruit and vegetables production. During 2013-14 the total value of export of horticulture produce (36.94 lakh MT) from India to different countries was Rs. 14,365 crore (Anonymous, 2014).

Out of a total 142.1 million hectares of cultivated area in India, dry land accounts for 91.0 million hectares and irrigation is available for only 40% of the cultivated area and the remaining 60% is rainfed. About 12 % of India's total geographical area is hot arid zone and the extent of arid area is about 31.7 million hectares. Significantly more than 61% of the area falls in Rajasthan and extends to Haryana and Punjab (9%), Gujarat (20%) and some pockets in Andhra Pradesh, Karnataka and Maharashtra (10%). The arid regions are distinguished by low and unpredictable rainfall (100-420 mm year $^{-1}$), frequent droughts, high summer temperatures (45-50 °C), high wind velocity (30-40 km h^{-1}), and high evapo-transpiration (1500-2000 mm year⁻¹). The sandy soils have poor fertility and low water retention (Bhansali et al., 2003). Decreased snowfall during winter created low chilling conditions in temperate areas, which is a serious threats to apple production in temperate areas in India (Singh et al., 2010).

Water stress can be very critical for the yield response during particular phenological phages and is very important in scheduling irrigation in considerable water limiting areas (Jones, 2004). In perennial fruit crops, stress before or during the flowering and post-bloom periods have adverse effects on yields through decreased numbers of fruits and reductions in cell numbers of the remaining fruits (Powell, 1974; Powell, 1976). Later stresses will typically reduce final fruit size or quality more than total yield. These factors have led to grower recommendations that irrigation is most critical in the early season (Goldhamer, 1988).

The perennial fruit trees provides opportunity because a mature tree already have a supporting structure of branches, it can rapidly grow a full canopy of leaves in the spring to maximize light interception and provide spurs for fruiting in coming year. Undesirable vegetative growth must be pruned out. Therefore, imposing moderate water stress to

reduce vegetative growth may have no negative effect on photosynthetic efficiency. Reduced canopy development (foliage growth) is one of the earliest responses to water stress, occurring before stomatal closure and reduction of photosynthesis (Bradford and Hsiao, 1982). In fruit trees the major objective is to divert these carbohydrates into fruit growth as fruit growth tends to dominate over vegetative growth (Higgs and Jones, 1991).

Vegetables crops are sensitive to drought stress owing to succulent nature. Furthermore, legume vegetables such as pea, cowpea, Indian beans, etc., cultivation in arid and semiarid regions are adversely affected by drought at the reproductive stage. Drought stress activates drought tolerance mechanisms by defined morphological, physiological and biochemical modifications in horticultural crops, which are investigated thoroughly for developing drought resistance varieties with greater potential to maximize water use efficiency.

Drought stress severely affects growth and yield and productivity of banana by reducing photosynthetic capacity of the plants. Water deficit during the period of finger development inhibits the translocation of assimilates to bunches (Surendar et al., 2013). Plant adaptation to different water availability conditions determines the magnitude and intensity of their physiological responses (Gurovich and Hermosilla, 2009; Oyarce and Gurovich, 2010). Birhanu and Tilahun (2010) reported that in tomato total plant biomass decreased with stress level while the fruit dry matter increased. Consequently, fruit dry matter weight increased and plant dry matter weight was decreased with stress level. The harvest index of *Melka Shola* was higher than that of *Melkassa Marglobe* at a particular stress level. In tomato, number and size of fruits were noted to reduce with moisture stress. The incidence of sunscald and blossom end rot was higher in the more stressed plants (75% ETc) deficit. The total soluble solid (TSS) content was significantly affected by irrigation treatments and increased with stress level whereas the fruit water content was decreased. Halil et al. (2001) reported that water stress resulted in significant decreases in chlorophyll content, electrolyte leakage, and leaf relative water content and vegetative growth. Severe water stress (40% of PC) reduced plant height by 46%, stem diameter by 51%, total dry weight by 43% and relative leaf expansion rate by up to 75%. In water stressed plants, root to shoot ratio was found 2.1 times more, indicated that water stress in eggplants change the pattern of dry matter distribution and produce longer roots. Plants grown under severe drought produce less yield and poor quality as compared to control treatment.

Drought is frequently accompanied by reasonably high temperatures, which increase evapotranspiration and affects photosynthetic activities, consequently intensifying drought reduce crop yields (Mir et al., 2012). Drought stress modifies photosynthetic rate, relative water content, leaf water potential, and stomatal conductance. Finally, it destabilizes

the membrane structure and permeability, protein structure and function, leading to cell death (Bhardwaj and Yadav, 2012). Drought is the one of the major abiotic stresses limiting banana production. Productivity is affected by water stress because of the early closure of stomata. Water potential is estimated by the exuding latex technique and demonstrate a small change in plants experiencing soil water deficit (Turner and Thomas, 1998) supporting the hydrated status of banana leaves although the soil is dry. Water deficit during the fruit development phase may affect their physiology and morphology and also influence susceptibility to weight loss during storage. Kensington mango fruit is more susceptible to postharvest chilling injury with exposure to water stress during the cell expansion phase of growth rather than stress given during cell division and near to harvest maturity. Therefore, it is vital to avoid water stress during fruit development when fruits have attained full size to facilitate reduced chilling injury in storage.

3. Mechanism of Drought Stress Tolerance

Drought tolerant plants adapt to water stress through various mechanisms like reduction in water loss by reducing stomatal conductance or morphological modification, improving water uptake by developing efficient root systems and accumulation of osmolytes. The osmolytes accumulated include amino acids- proline, amines- glycinebetaine and dimethylsulfonioppropionate, polyol- mannitol and trehalose and sugars like sucrose and oligosaccharide. Sugar plays important role in osmoregulation under water stress in many plants such as alfalfa and *Ziziphus mauritiana*. These compounds play a key role in preventing membrane disintegration and enzyme inactivation in the low water activity environment. Water deficit decrease the turgor of guard cells of the stomata and which closes the stomata and reduces the rate of transpiration. Water deficit elevate the levels of abscisic acid (ABA) from the mesophyll cells, which transferred to guard cell and keep stomata closed. It is an interaction between precipitation, evapotranspiration, irradiation, soil physical properties, soil nutrient availability and biological interaction (Turner, 1972). Mechanism of drought tolerance can be grouped into three categories, viz. drought escape, drought avoidance and drought tolerance (Leonardis et al., 2012).

3.1. Drought escape

These plants become dormant during drought period and complete their life cycle during favourable moisture condition. The ability of a crop plant to complete its life cycle before development of serious soil and plant water deficits is called as drought escape. This mechanism involves rapid phenological development i.e. early flower production and fruit maturity, difference in duration of growth period depending on the degree of water stress. In Robusta coffee clone, defoliation due to water deficit stress occurred successively from older to

younger leaves, conforming that the more drought sensitive the clone, the greater the defoliation (DaMatta, 2004). For instance, in cow pea early erect cultivars, such as "Ein El Gazal" and "Melakh", have performed well when the rainfall season was short but distinct due to their ability to escape late-season drought (Hall, 2004). But the genotypes of short duration are less productive compared to that of normal duration.

3.2. Drought avoidance

These plants do not come to thermodynamic equilibrium with the stress or can exclude the stress by morphological modifications. In this group, plants maintain high water potential that results from either reduction of water loss or maintenance of water uptake. Plants naturally transpire and lose a significant amount of water through stomata. These plants are again divided in two groups i.e. water savers and water spenders.

3.2.1. Water savers

Plants maintain high water potential through a reduction in absorption of radiation or reduction in leaf area. Increase in stomatal or cuticular resistance reduces water losses and angle of inclination to incoming radiation provides less area for absorption. Leaf colour and reflecting properties, development of waxy cuticle and pubescence helps in reduction in water loss.

3.2.2. Water spenders

Water spender plants maintain high water potential by spending more water through efficient root system. These plants have deep root system, sparse root and branches and high root hairs for reabsorption of water. The pattern of root growth also changes in response to water availability. The more elaborate the root system, the greater the chance that the plant will survive during water stress (Hu, 1992; Wade et al., 1996). Arid fruit crops like ber, lasoda, bael, custard apple, phalsa, datepalm and tamarind are grown in xerophytic conditions. Drought avoidance mechanisms are associated with morpho-physiological modification such as leaf area reduction, stomatal closure and cuticular wax formation, and changing root depth and its density, root hair expansion and hydraulic conductance in root which decrease radiation adsorption and transpiration (Beard and Sifers, 1997; Rivero et al., 2007). In monocots leaves roll up during dry weather. In banana, higher accumulation of dry matter to the roots results in a high root to shoot ratio in water stressed plants (Ismail et al., 1994). Reducing the number of leaves could be a phenomenon by the plants to minimize the transpiration surface. All of these strategies protect plants during water deficit condition, but they also reduce photosynthesis and are harmful to the survival of plants over long periods of drought. During water deficit stress ber effectively manage water loss by reduction in leaf area and stomatal closure resulting in higher intrinsic water use efficiency (Jones, 1992).

3.3. Drought tolerance

Drought tolerant plants have capacity to tolerate drought at

low water potential. Drought tolerance is achieved by cell and tissue specific physiological, biochemical and molecular mechanisms, which include specific gene expression and accumulation of specific protein. The ability of a plant to produce its economic product with minimum loss under water deficit environment in relation to the water constraint-free management is referred as drought tolerance (Mitra, 2001). Drought tolerant plants are classified in two categories as dehydration avoidance and dehydration tolerance.

3.3.1. Dehydration avoidance

This category plant tolerate drought by maintaining high turgor by decreasing their osmotic potential due to accumulation of solutes and this phenomenon is known as osmotic adjustment or osmoregulation. The smaller cell size and high elasticity helps in maintaining turgor potential. Drought tolerance through increased solute absorption responsible for osmotic adjustment may have harmful effect apart from energy required for osmotic regulation (Turner, 1979).

3.3.2. Dehydration tolerance

This category plant tolerate drought at negative turgor. Many lichens, bryophytes and few fern can survive in dried state. Resurrecation plants are almost completely dehydrated and they recover when they are rehydrated such as Maruthymus. Drought tolerance has been considered as a valid screening of banana germplasm for water deficit target to partially compensate for the loss in yield. The B genome contributes to drought tolerance in banana (Turner, 1995; Thomas and Turner, 1998). In certain situations, such as extended periods of drought, plants cannot avoid a decrease in water potential. Drought tolerance mechanisms can involve different pathways inside the cell, but the end result is expression of stressresponse genes. These pathways includes osmoprotectants, ion exclusion, ion export, cell membrane modification and antioxidant enzyme systems. Phenotypic traits associated directly with drought tolerance are unclear; however, several (Ludlow and Muchow, 1990; Jongdee et al., 1998) investigations noted that osmotic adjustment is associated with drought tolerance. Therefore, crop adaptations to drought may be established through a balance between escape, avoidance and tolerance while maintaining adequate productivity in horticultural crops.

4. Morphological Modification

Water stresses cause modification in morphology through a wide variety of change in plant growth, leaf morphology and movement and root development and finally productivity.

4.1. Plant growth

The water stress slow down the plant growth and development more than any other environmental factor. Sprouting and germination of seeds are adversely affected by drought and which create poor plant establishment. Cell growth is considered one of the most drought sensitive processes due to the reduction in turgor pressure. Under water deficiency,

cell elongation of higher plants can be inhibited by interruption of water flow from the xylem to the surrounding elongating cells (Nonami, 1998). Drought caused impaired mitosis; cell elongation and expansion resulted in reduced growth and yield traits (Hussain et al., 2008). Water stress condition reduce the leaves size and number per plant, leaf life by reducing the soil's water potential. Leaf area development depends on leaf turgor pressure, temperature, and food supply for growth and development. Drought stimulated reduction in leaf area is attributed to reduction of leaf expansion through inhibited photosynthesis (Rucker et al., 1995).

4.2. Leaf morphology and movement

Leaf characteristic such as leaf size, shape, angle to incoming radiation are the important factors for determining tolerance to water stress. Leaf thickness, hairiness, increase in size of protective and mechanical tissues and mesophyll integrity are the important criteria for drought tolerance in wheat. Under water stress thickness of cuticle, epidermis, hypodermis and number of stomata increased, while number of hairs and stomatal length decreased (Hameed et al., 2002). Leaves reduce net radiation by changing leaf angle from horizontal to angular position. Leaf rolling, leafless or greenish stem, light whitish colour and more number spines are important features of xerophytes which help in combating drought stress in horticultural crops such as in ber, aonla and ker.

4.3. Root development

Root development is strongly influenced by moisture deficit (Sangakkara et al., 2010). This is true even for drought-tolerant species such as *Manihot esculentum* (Sriroth et al., 2001). The drought stress effect is generally high on shoot growth than on root growth. This lower sensitivity of roots appears to occur as a consequence of the rapid osmotic adjustment of roots in response to a decrease in soil water-content, which allows the maintenance of water uptake, and is also due to the enhanced loosening ability of root cell walls (Sharp et al., 2004). Therefore, a decrease in the shoot: root ratio under drought stress is a frequently observed phenomenon, which is due to an increase in root growth and relatively severe inhibition of shoot growth than root growth (Franco et al., 2006). This was the case with *Capsicum annuum* (Kulkarni and Phalke, 2009), *Nerium oleander* (Niu et al., 2008), *Opuntia ficus-indica* and *Opuntia robusta* (Snyman, 2004), rose (*Rosa multiflora* and *Rosa odorata*) rootstocks (Niu and Rodriguez, 2009). Apart from the shoot:root ratio, root characteristics like root length, fresh and dry weight, root surface area, root depth and cortex thickness and root behaviour like root turnover, metacutisation, hardening, and hydraulic conductivity are sturdily influenced by drought. Plants facing water deficit develop a more extensive root system to capture the available water such as ber, bael, aonla and ker. This was the case with *Phaseolus vulgaris*, as reported by De Sousa and Lima (2010), who found an increase in root length under drought stress. Huang (2008) found that long root system was

essential to maintain cellular hydration by avoiding waterstress in turf-grass.

4.4. Epicuticular wax

The plant cuticle has a significant role in protecting plants during water stress. The cuticular layer consists of lipids and polysaccharides. The cuticle layer is covered by a smooth amorphous wax film. Cuticular wax form a layer with considerable ultra-structural and chemical variability. Epicuticular waxes are composed of a mixture of chemical compounds: hydrocarbons, primary alcohols, aldehydes. They reduce the loss of water, reflect or reduce radiation absorption, form the basis of phyllosphere, protect plant tissues against penetration by fungi, bacteria and insects, as well as damage by wind, rain, soil particles etc., reduce water retention on the plant surface, and provide a self-cleaning surface. Shivasankar et al. (1993) reported that the level of epicuticular wax was higher in stress condition. During drought stomata get closed and water loss occurred through the leaf cuticle without CO₂ fixation. Higher deposition of ECW decreased cuticular permeability of water loss and increases the crop albedo (Blum and Ebercon, 1981). In arid horticultural and other crops, drought resistance is highly influenced by the thickness of the epicuticular wax layer and varieties having a thick cuticle layer were reported to retain their leaf turgor for longer periods during water stress.

5. Physiological Changes

A plant counters to water stress by reducing growth and photosynthesis and other plant processes in order to reduce water use. As water loss increases, leaves of some species may change color usually to bluegreen or whitish. Foliage begins to wilt and leaves fall off and the plant die. Drought lowers the water potential of a plant's root and abscisic acid is accumulated and ultimately stomatal closure occurs. This reduces a plant's leaf relative water content. The time required for drought stress to occur depends on the waterholding capacity of the soil, environmental conditions, stage of plant growth, and plant species. Ogbaga et al. (2014) reported that plants growing in sandy soils with low water holding capacity are more susceptible to drought stress than plants growing in clay soils. A restricted root system will increase the rate at which drought stress develops. A root system may be restricted by competing root owing to compacted soils, high water tables and container size. A plant with high mass of leaves with respect to the root system is more prone to water stress as leaves lose water faster than water supply by the roots. Newly established orchards are susceptible to drought stress because of the poor root system development and high foliage growth in initial stage. Plants adapt to water stress through various physiological mechanisms such as changes in chlorophyll content of leaf tissue, chlorophyll and membrane stability, relative water content of tissues, osmotic potential (OA), stomatal conductance, transpiration, photosynthesis, poly phenol oxidase (PPO), reactive oxygen species (ROS) and antioxidant defense.

5.1. Photosynthetic pigments

Chlorophyll is one of the major chloroplast apparatus for photosynthesis activity in plants. The decrease in chlorophyll content under drought stress has been reported and it may be the result of oxidative stress and chlorophyll degradation. The chlorophyll content of leaf tissue varies with cultivars, age of the crop, growth stages, light and temperature (Kumar and Singh, 1996). Makhmudov (1983) reported that moisture stress inhibited biosynthesis of the precursor of chlorophyll in wheat leaves which ultimately reduced the chlorophyll content. Chen and Creeb (1991) found increased level of carotenoid content under drought conditions. The chlorophyll content of the leaf was decreased by water deficit but there was accumulation of large amount of proline in the leaf. Asharaf and Mahmood (1990) reported that total chlorophyll content of the leaf declined under water stress conditions. It may be due to decreased synthesis and increased degradation of chlorophyll in leaves under water stress (Dekov et al., 2000).

5.2. Chlorophyll stability index (CSI)

Chlorophyll stability index (CSI) is the stress tolerance capacity of plants and measured through integrity and stability of chlorophyll. Mohan et al. (2000) reported that high CSI value means that the stress did not have much effect on chlorophyll content of plants. Plants having higher CSI can withstand stress owing to better availability of chlorophyll, leading to increased photosynthetic efficiency under stress.

5.3. Membrane stability index (MSI)

The membrane integrity and functions is influenced by reduced water content under water stress and measured through membrane stability index. The estimation of cellular electrolytes leakage from stressed leaf tissues into an aqueous medium is measure of MSI and used for drought resistance. Crop varieties differ in dehydration tolerance by the cell membrane capacity to prevent electrolyte leakage at decreasing water content. MSI is correlated with yields under high temperature and also possibly under drought stress. Preservation of membrane integrity and functions under a dehydration stress has been used as a measure of drought tolerance by various researchers (Premachandra et al., 1990). Selection for osmotic membrane stability, root length and root to shoot length ratio under osmotic stress could be instrumental in predicting the drought tolerance of genotypes (Dhanda et al., 2004).One of the primary injuries caused by water stress is loss in cell compartmentation due to the disruption of membrane stability. Increased leakage of solutes is an indication of damage caused to membrane. Upadhyaya et al., (1989) found that the decrease in MSI estimated by taking comparative ion leakage is an indicator of membrane damage as a result of lipid peroxidation caused by reactive oxygen species (ROS). Lower membrane injury and hence lesser amount of solute leakage reported in chickpea

cultivars under water stress.

5.4. Relative water content (RWC)

Relative water content is the suitable measure of plant water status in terms of the physiological consequence of cellular water deficit. Water potential indicates plant water status and play important role in water transport in the soil-plantatmosphere continuum. RWC is an appropriate estimate of plant water status in terms of cellular hydration under the possible effect of both leaf water potential and osmotic adjustment (Barrs and Weatherly, 1962). In banana, Mohd Razi et al. (1992) observed a significant reduction in both photosynthesis and transpiration as a result of drop in leaf water potential below 2.0 MPa. Natarajan and Kumaravelu (1993) reported that drought resistance varieties showed consistently higher leaf water potential in their tissues than susceptible types under soil moisture deficit.

5.5. Osmotic adjustment (OA)

Plants accumulates various osmolytes like proline, aminesglycine-betaine and dimethylsulfonioppropionate, polyolmannitol and trehalose and sugars like sucrose and oligosaccharide in response to water stress which lowers of the osmotic potential and helps in maintaining turgor potential. This is termed osmotic adjustment and enables the plant to take up water, maintain turgor and survive longer (Ogbaga et al., 2014). Osmotic adjustment is considered as an important physiological mechanism of drought adaptation in many plants (Subbarao et al., 2000). Milburn (1993) found that in the water relations of the banana, the latex exudations were found to be the useful guide in determining the water potential of the plant. In banana, the solute potential of exuding latex provided an excellent guide to the water status of the plant during water deficit conditions (Kallarackal et al., 1990). Zlatev (2005) observed that osmotic adjustment is one of the major adaptive mechanisms of *Phaseolus vulgaris* to survive drought. The bean genotypes displayed significant differences in their adaptive response to drought. High osmotic adjustment was found in cultivars Plovdiv 10 and Prelom. The main difference among cultivars appears to be due to turgor maintenance, which may be more representative of the physiological status of the leaves in these cultivars.Osmotic potential of cherry cultivar Colt and Meteor at full turgor was decreased owing to water stress from leaves and roots (Ranney et al., 1991). Glucose has been found directly associated to osmotic adjustment in *Fragaria chiloensis* (Zhang and Archbold, 1993).

5.6. Stomatal conductance

Stomata play a major role in water relations and photosynthesis of the plant. This is also true for the water relations of banana, particularly of the Cavendish subgroup (*Musa* spp., group AAA) (Brun, 1961). Kumar and Singh (1996) observed a positive correlation between stomatal diffusive resistance and water stress.

5.7. Transpiration rate

Water stress results in loss of turgidity of guard cell along with reduction of cell size and leaf area which helps in closing of stomata and decrease in transpiration rate. The rate of transpiration is directly related to difference between water vapour concentration in the intercellular spaces of the leaf and the ambient air. Pejic et al. (2014) concluded that the onion bulb yield under rainfed conditions (1554 kg ha⁻¹) was significantly lower than the yield (3555 kg ha $^{-1}$) recorded under irrigation conditions. Evapotranspiration rate under irrigation conditions ranged from 448.9 to 511.9 mm, while it varied from 290.2 to 393.9 mm under non-irrigation conditions.

5.8. Photosynthesis

Water stress is one of the most important environmental factors inhibiting photosynthesis (Bradford and Hsiao 1982). Tezara et al. (1999) reported that water stress substantially alters plant metabolism, decreasing plant growth and photosynthesis and finally crop productivity. Water stress restricts diffusion of CO₂ into the leaf, due to stomatal closure and inhibits of CO₂ metabolism. Stress decreases the amounts of ATP, and ribulose bisphosphate found in the leaves, correlating with reduced \textsf{CO}_2 assimilation, but the amount and activity of ribulose bisphosphate carboxylaseoxygenase (Rubisco) do not correlate. Rivas et al. (2016) suggested that the tolerant cow pea cultivar was able to maintain higher photochemical activity and leaf gas exchange during water deficit for a longer period than the sensitive cultivar, which could alleviate the stress effects to the photosynthetic machinery and improve its recovery ability. Berman and Dejong (1996) reported that water-stressed peach trees with heavy crop loads had significantly reduced fruit dry weights, which were likely due to carbohydrate source limitations occurred during high carbon demands of photosynthesis.

6. Biochemical Changes During Water Stress

Water stress cause a lot of biochemical changes in plant cell like accumulation of osmolytes, compatible solutes, biosynthesis of enzymatic and non enzymatic antioxidants.

6.1. Proline

Proline, an amino acid accumulates due to hydrolysis of protein under water stress conditions (Kramer, 1983). High proline accumulation during stress was noted as an adaptive mechanism by which it served as a store of nitrogen and respiratory substrates to facilitate post stress recovery (Dix et al., 1986). Kala and Godara (2011) found that during the stress period the total proteins decreased with increase in stress in the leaves of all the three cultivars, and the decrease was maximum in Kaithli followed by Gola, but the proline accumulation in the cultivars was increased during stress period. The proline accumulation in Gola accumulated at faster rate than Umran and Kaithli.

6.2. Reactive oxygen species (ROS)

Drought creates imbalance in light capture and its utilization,

which inhibit photosynthesis and make imbalance in generation and utilization of electrons and finally results in generation of reactive oxygen species (ROS). The production of ROS in plants is an early event of plant defense response to water-stress and acts as a secondary massager to trigger subsequent defense reaction in plants. Reactive oxygen species include oxygen ions, free radicals and peroxides, byproduct of the normal metabolism of oxygen and play important function in cell signaling. Though, during drought, ROS levels increase considerably resulting in oxidative damage to proteins, DNA and lipids (Apel and Hirt, 2004). Highly reactive ROS can adversely affact plants by increasing lipid peroxidation, protein degradation, DNA fragmentation and causing cell death. Plants produce H_2O_2 in metabolic processes and cause damage of cell oxidation function. The enzyme, catalase (CAT) eliminates H_2O_2 and plays a key role in the elimination of active species of oxygen (O₂-). The free radicals (OH⁺, O₂-) generated during lipid peroxidation readily reacted with protein and lipid membrane causing cell damage (Elstner, 1991).

6.3. Abscisic acid (ABA)

Abscisic acid syntheses is one of the first reactions of plants to water stress, stimulates ABA-inducible gene expression and cause stomata closing, in that way reducing water loss through transpiration and ultimately limits cell growth. The ethylene receptor genes are upregulated by low O_2 and ethylene play a crucial role in anatomical and physiological effects during hypoxia/anoxia. During O_2 depletion, ethylene accumulation down regulates ABA by inhibiting rate limiting enzymes in ABA biosynthesis and by activating ABA breakdown to phaseic acid. Water deficit is sensed by the roots inducing a signal to the shoots through xylem causing physiological and morphological changes. Several genes are regulated with osmotic stress and majority of these responsive genes can be driven by either an ABA dependent or ABA independent pathway. Some studies suggest that ethylene shuts down leaf growth very fast after the plant senses limited water availability. Ethylene accumulation can antagonize the control of gas exchange and leaf growth upon drought and ABA accumulation (Carolina et al., 2015).

6.4. Poly phenol oxidase (PPO)

Cano et al. (1997) reported that poly phenol oxidase has been investigated in banana for browning reaction. The PPO is widely considered as a plastid enzyme although it was reported in the cytoplasm of fruit tissues during ripening followed by senescence. Reduced activity of PPO was recorded during low temperature stress in *Ipomoea aquatica* (Ose et al., 1999). Poly Phenol Oxidase is responsible for the enzymatic browning reaction occurring in many fruits and vegetables damaged by improper handling, resulting in bruising, compression or indentations. The PPOs are very important enzymes in the food industry, due to their involvement in the enzymatic browning impairs the sensory properties and marketability of the product and also lowers the nutritional

value (Ramirez and Mehraj, 2004).

7. Molecular Mechanism During Water Stress

At molecular level various changes takes place including biosynthesis of osmolytes and PGRs and stress-responsive genes expression etc. Different high throughput techniques like genetic engineering, transcriptomics, proteomics, metabolomics and mutation analysis are applied for stress tolerance induction.

7.1. Biosynthesis of osmolytes

The active accumulation of osmolytes in the cytoplasm of plants decreases osmotic potential and maintains turgor potential. Many horticultural crops not synthesize the special osmoprotectants that are naturally accumulated by stresstolerant organisms. The genetic engineering of metabolic pathways for the production of osmolytes such as mannitol, glycinebetaine, proline and trehalose etc. might increase resistance to drought (Ramanjulu et al., 2002).

7.2. Stress responsive genes

Gene isolation and cloning through molecular biology research are based on RNA or protein expression, differential screening, DNA insertions such as transposon or T-DNA insertions, map based cloning and methods of random cDNA sequencing and genome sequencing. The recent expansion in activities concerned with identifying genes with unknown functions through research on expressed sequence tags (ESTs) and sequencing of total genomes is a boon for abiotic stress-related work. In Carrizo Citrange introduction of p5cs gene induced more accumulation of proline in leaves which improved drought tolerance (Molinari et al., 2004).

7.3. Functional genomics

This technique uses high throughput techniques like genetic engineering, transcriptomics, proteomics, metabolomics and mutation analysis to explain the function and interactions of genes. The recent discovery of promoter regulatory elements, like DRE or ABRE involved in both water stress and low temperature induced gene expression in *Arabidopsis,* as well as the identification of transcriptional factors interacting with those promoters, are exciting developments. It makes use of huge data produced by genome sequencing to describe genome function. Encoding of transcription factor was improved drought stress tolerance in transgenic apple (Pasquali et al., 2008). Transgenic apple Royal Gala plants over expressed a ascorbate peroxidase gene which indicated improved drought tolerance (Wisniewski et al., 2008).

7.4. Plant growth regulators

In plants, ABA synthesis is one of first reaction to water stress, which activate ABA-inducible gene and causing stomatal closure, thereby minimizing transpirational loss and finally limiting cellular growth (Yamaguchi-Shinozaki and Shinozaki, 2006; Wilkinson and Davies, 2010). Many ABA-mediated physiological processes induced by water deficit, including closure of the stomata and acceleration of leaf senescence, are counteracted by cytokinin which delay ABA-induced stomatal closure. It has been observed that in plants longterm reaction to stress, hormones such as ABA and cytokinin may regulate the production, metabolism and distribution of certain metabolites essential for stress tolerance mechanism (Pospisilova and Dodd, 2005; Stoll et al., 2000).

8. Breeding for Drought Tolerance

An understanding of genetic basis of drought tolerance is a pre-requisite for breeders to develop superior genotype by adopting conventional breeding methodology. Besides morphological and physiological changes, biochemical changes involving biosynthesis of compatible solute is another way to impart drought stress tolerance. Responses of different genotypes to water deficit condition have been studied for a long time, and several morphological, physiological and biochemical characters have been suggested to be responsible for drought tolerance. In banana, some of the cultivar groups with the *balbisiana* (B) genome are considered to be relatively tolerant of seasonal drought (Price, 1995; Simmonds, 1995). Among the horticultural traits, although number of pods per plant had shown good narrow sense heritability and genetic advance under drought, but leaf water potential appeared to be better indicator for selection criteria owning to higher heritability under drought stress in okra (Ben-Ahmed et al*.*, 2006; Naveed et al., 2009). Source genotypes having resistance or tolerance to drought stress are identified for strengthening breeding programme (Table 1). Some of the fruit and vegetable varieties (Table 2) are developed by using these drought resistance or tolerance genotype.

8.1. Marker assisted breeding

There are a large number of genes and proteins associated with stress tolerance in plants and so the best approach to identifying stress tolerant lines through quantitative trait loci (QTL) analysis. Molecular engineering for stress resistance in fruits and vegetables is limited due to the complexity of the stress response network means that modulating the stress resistance with single gene insertions is unlikely and methods to successfully transform many important fruit and vegetable crops need to be developed.

9. Management of Water Stress in Horticultural Crops

Some of the most common ways of management of water stress in horticultural crops includes development of resistance/tolerant genotype and conserving moisture through various horticultural practices are discussed below;

9.1. Germplasm selection

Short duration varieties, having efficient root system and capacity to recoup after the alleviation of stress need to be selected. The fruit crop selected for water deficit or arid region should be such that its maximum growth period

Table 2: Drought tolerant variety/ lines of fruit and vegetable crops

synchronizes with the period of maximum water availability. Preferably the flowering and fruiting must be completed well before the commencement of water deficit. Fruits crops like ber, lasoda, pomegranate, custard apple, aonla, acid lime, mosambi, phalsa, bael, wood apple, jamun, karonda, date palm and fig are best suitable for arid region cultivation. The germplasm selected should have drought tolerance mechanism like deep root system (bael, ber, date palm), leaf

shedding (ber, gonda), presence of thorns (ker, karonda), stomata at lower side (custard apple), wax coating (ber), sparse foliage and leaf orientation (aonla), water binding mechanism (fig), hairyness and sunken stomata (fig, phalsa, ber and lasoda). Intense solar radiation is important feature of arid region and crop like kinnow mandarin can be selected which has tolerance against drought and bear fruits inside well formed canopy (Chundawat, 1990).

Germplasm/variety should be short in duration. Gola and Seb in ber, Ganesh, Bassein seedless and Jalore Seedless in pomegranate and Halawy and Barhee in date have been found to be promising in arid region. Besides, there are many indigenous drought hardy plants which has characteristics like deep root system (bael, tamarind), stay green and scanty foliage (kair), musilagenous sap in plant parts (kair, lasoda, pilu, bael). Some of the drought tolerant varieties in fruit crop are Ruby in pomegranate, Arka Sahan in custard apple, Deanna and Excel in fig and Karpuravalli and Kanthali in banana (Bose, 1996). In vegetable crops like cluster bean, moth bean, cowpea, lima bean, chilli, drumstick, brinjal, okra are suitable for rainfed cultivation. Among these, legume vegetables can be recommended for contingency cropplanning in case of late monsoon rains.

9.2. Use of stress tolerant rootstocks

Some fruit plants are susceptible to drought/saline/sodic stress conditions, but with the use of appropriate stress tolerant root stocks, their cultivation is possible under stressed conditions to a great extent. Rootstock must possess deeper root system and should have capacity to reduce/selective absorption of cations/anions. Commonly identified rootstock for various stress situations are presented in Table 3.

9.3. Agronomic measures

Contour cultivation, contour trip cropping, mixed cropping, tillage, mulching and zero tillage are some of the agronomical practices for the *in-situ* soil moisture conservation. Mechanical actions like contour farming, bench terracing, mulching and water harvesting recycling etc. also required to be practiced for effective soil and moisture conservation in arid and semi arid regions. Rainwater harvesting includes collecting runoff water into dug out ponds or tanks in small depressions, gullies and into storage dams or masonry structures. Mulching is also practiced in horticultural crops using crop residues and other organic material farm waste. Mulches helps in conserving the soil moisture during critical stages of water requirement and reduced the weed population. The polythene mulch maintained 29% more soil moisture compared to unmulched trees on soil available water content basis (Sharma, 2007; Chandrasekharan and Pandian, 2009). Straw mulch ameliorates environmental stresses and improves the product quality and safety (Jat et al., 2006). In vegetable cultivation, 25-30 micron thickness and 1 to 1.2 m width polyethylene mulch is used. Generally raised bed with drip irrigation system is followed for mulching.

Table 3: Abiotic stress tolerant rootstocks in horticultural crops

Source: Pathak (2004); Saroj (2009); Nimbolkar et al., 2016

9.3.1. Canopy management

Transpiration is essential to plant life, and is controlled by the balance between water availability in the soil and the demand for water from the environment. A key determinant of demand is the area of leaves or canopy size. Reducing canopy size can result in significant reductions in water demand, through the physical removal of transpiration sites. The size of the canopy is directly related to water demand.

9.3.2. Wind breaks

The adverse effect of high temperature and dry winds can be overcome by planting, tall growing trees along the farm boundary. Windbreaks help in reducing the velocity of wind and reduce transpiration and evaporation losses along with development of suitable microclimate. The orientation of windbreak should be at right angles to the prevailing winds. It is believed that the windbreak is effective for a distance equivalent to 3 to 4 times of tree height (Chundawat, 1990). *Acacia tortalis, Cassia siamea* and *Prosopis julifera* are some of the useful tree species suitable as wind break under less water conditions. But on economic and soil conservation point of view *Sizium cumini*, *Prosopis cineraria* and *Ziziphus numuleria* can also be used as windbreak in arid region.

9.3.3. Soil organic matter

Constant efforts must be made to improve the soil organic carbon. Incorporation of crop residues and farm yard manure to soil improves the organic matter status and improves soil water holding capacity. Soil organic matter content is improved by adopting crop rotation, green manuring and involving

agro forestry crops. Vegetables are short duration crop with faster growth phases; therefore, organic matter required to be properly decomposed. Vermi-composting is practiced for faster usage of available organic matter in the soil and improving the moisture holding capacity of soil.

9.3.4. Foliar nutrition

The foliar spray of nutrients during drought conditions helps in the better growth by faster absorption of nutrients. The K and Ca spraying induce drought tolerance in fruits and vegetable crops. Spraying of micronutrients and secondary nutrients improves crop yields and quality.

9.3.5. Drip irrigation

Drip irrigation is most efficient method of irrigation in horticulture due to precise and direct application of water to root zone. A significant saving in water (30-50%), higher yields of fruits and vegetables and control of weeds, saving in labour and fertigation under drip irrigation are the additional advantages. Drip irrigation is highly successful in fruit crops and also adopted in vegetable crops including low spaced crops like onions and beans. Generally inline drip laterals having emitting point spaced at 30cm distance and emitting at the rate of 2 litres per hour is selected for vegetable crops. In chilli, brinjal, cauliflower and okra paired row planting is followed and one drip lateral is sufficient for two crop rows. Studies on methods of irrigation in capsicum, tomato, okra and cauliflower suggested that by adopting alternate-furrow and widely-spaced furrow irrigation has saved 35 to 40 % of irrigation water without reduction in productivity. It has been found that up to 81% water saving was observed in lemon compared to flood irrigation with the over 35% increase in yield. Similarly, banana, grapes and pomegranate recorded 45% saving in water using drip irrigation.

9.4. Protected cultivation and seedling production

Improved method of seedling production such as protray grown seedling using coco peat, polytunnel, nylon net protection, bio-fertilizers and bio-pesticide inoculation at nursery stage has good potential for obtaining hardy, uniform and healthy seedlings. These seedlings after transplanting field produce better root system with less root damage and overcoming water stress conditions. In regions where climate does not favour year round production of crops in the open field, vegetable production can be taken up in protected environment. Protected cultivation protect crop from biotic and abiotic constraints. The yield of tomato, onions and melons are severely affected during high rainfall due to foliar diseases, lack of proper soil aeration, physical damage of the foliage and flower drop. Net house cultivation and shade net cultivation provide better microclimate especially during summer in minimizing the high temperature effect and improving the relative humidity. The yield of tomato, cucumber and capsicum can be improved during high temperature period by covering with net/shade net.

9.5. Regulated deficit irrigation and partial root zone drying (PRD)

Deficit irrigation (i.e. irrigation below optimal crop water requirements) is applied to improve productivity of horticultural crops to control excessive vegetative vigour in high-density orchards. Now a days, controlling excessive vigour to stimulate improvements in fruit and vegetable quality so that any yield loss can be compensated by an increase in crop value (Costa et al., 2007; Stefanelli et al., 2010). When a part of the root zone dries out, ABA produced in the roots in drying soils and is transported by water flow in xylem to the shoot for regulating the shoot physiology. The increase in ABA in the xylem flow roots to leaves triggers the closure of stomata as response to water stress and reduced shoot growth and transpiration. In fruit crops flowering, fruit setting and development are critical stages for water stress which effects production adversely and drastic reduction in yield have been noticed. In vegetable crops like cauliflower, cabbage, broccoli critical stage is head formation and enlargement; and in potato-tuber set & enlargement, onion- bulb enlargement, sweet potato-root enlargement; cucumber, tomato, pepper, eggplant- flowering, fruit set and enlargement are the critical stages for water stress that should be considered during scheduling irrigation. In pomegranate for flower regulation plants are subjected to water stress. Irrigation is withheld onetwo months prior to the *bahar* which result in leaves wilting and defoliation (50-70%). The principle behind withholding of irrigation is to provide rest to the plant, which results in accumulation of food in large quantity for enhancing flowering in ensuing season. Flower regulation manipulate the natural flowering and fruiting in pomegranate and produce higher yield with quality fruits in desired season with sustainable use of farm resources (Kumar et al., 2019). Partial root zone drying technique is successfully used in commercial grape cultivation to reduce vine growth and water use and producing crop yield, and berry size and improving fruit quality as against conventional irrigation (Dry and Loveys, 1998).

9.6. Uses of anti-transpirants

Anti-transpirants are chemicals sprayed on plants to form a film which increases the diffusion resistance of water from stomata and thus reduces transpiration losses of water. Several chemicals have been successfully used like acropyl in grapes, polycot in banana and kaolinite (3-8%) in different fruit plants. The energy input can be reduced by increasing plant reflectivity by using effective chemicals like zinc oxide, kaolinite, chalk etc alone or in combination with other anti-transpirants. These chemicals are used to reduce temperature on plant parts. Film forming compounds like wiltpruf, mobileaf, clear spray, vapour gard and folicoat can be used to reduce transpiration and water loss. Water loss can also be restricted by applying chemicals which facilitate stomatal closure. Some of these are; phenyl mercuric acetate (PMA), decenyl succinic acid (DSA), atrazine and sodium azide.

9.7. Use of plant growth regulators

The anti-ethylene products such as aminovinylglycine (AVG) and 1-methylcyclopropene (1-MCP) could be used to mitigate drought stress. While foliar cytokinin application can prevent ABA-induced photosynthetic limitation, the effects can be transient and of little consequence in the long term. Paclobutrazole (10 mg \vert ⁻¹) is used to avoid moisture stress in mango and jasmonic acid applied in pear for drought tolerance by increasing the betaine level (Gao et al., 2004). Ethrel (1-2 ml/l) is applied in pomegranate for leaf shading during flower regulation treatment, which induce uniform flowering with improved sex ratio (Kumar et al., 2018).

9.8. Use of beneficial microbes

Microbes such as rhizobacteria and mycorrhizae can protect plants from the harmfull effects of flooding and drought. Rhizobacteria include mycorrhization helper bacteria and plant growth promoting rhizobacteria, which assist AMF to colonize the plant roots. Synergistic interactions have been reported between arbuscular mycorrhizal fungus and nitrogen fixing bacteria fluorescent *pseudomonas* and sporulating *Bacilli*. The generally found bacteria in the plant mycorrhizosphere are *Pseudomonas*. These mycorrhizal symbioses in vegetables, fruits increased growth and yield by increasing drought tolerant capacity. Arbuscular mycorrhizal fungus were observed in the citrus rhizosphere and provided drought tolerance in citrus crop (Singh et al., 2011). Arbuscular mycorrhizal fungus inoculation with *Glomus mosseae* significantly increased absorption areas of root systems in the Trifoliate orange seedlings grown at varying soil water contents as against without arbuscular mycorrhizal inoculation (Wu and Xia, 2006).

10. Drought Recovery

Horticultural crops can be recovered from water stress through use of recoverable germplasm and management practices. Recovery of a banana germplasm from drought is related to its ability to retain green leaf area during that period. Plants with good leaf retention can supply more assimilates to the developing fingers during subsequent recovery (Stover, 1972). A slow rate of onset of stress may allow for development of adaptive mechanisms such as osmotic adjustment, decreasing leaf area, abscission of leaves, leaf folding, rolling or reorientation of leaves and an increased root growth rate (Flore et al., 1985). Pejic et al. (2009) reported that out of the total amount of water used for sunflower evapotranspiration (ETm), 48% were spent during flowering, pollination, seed formation, seed fill, and ripening. As a result, irrigation scheduling of sunflower must be programmed to provide optimal soil moisture levels during the periods of flowering and yield formation. The irrigation should be performed to the start of flowering. Genotypic differences in drought tolerance of strawberry have been observed and cultivars 'Elsanta' found most adaptable to water deficiency conditions. Morphological and physiological adaptations facilitated 'Elsanta' plants to maintain growth and productivity when water availability was reduced. The plants of cultivar 'Honeoye' showed the lowest tolerance to water shortage (Klamkowski et al., 2015).

11. Conclusion

Moisture stress is one of the important factors in reducing yield of horticultural crops. Efforts should be focused on germplasm selection and improvement through morphological, physiological, biochemical and molecular understanding of drought stress. The identification of quantitative trait loci with effects on drought tolerance traits and transcription factors regulating drought response genes, their product and crosslink between different signaling components should be future research area. It is also important to reduce water use without significant losses in yield and quality.

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