Research Article

Mechanisms and Strategies for Improving Drought Tolerance in Fruit Crops

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Abstract

Climate change resulted in low water availability as well as increasing demands for food in the future makes breeding for drought tolerant crops a high priority. Drought stress is one of the most ominous abiotic factor limiting the productivity and quality of fruit crops resulting in huge economic loss to the fruit growers. Plants have developed diverse strategies and mechanisms to survive drought stress. Most of these represent drought escape or avoidance strategies like early flowering or low stomatal conductance that are not applicable in breeding for crops with high yields under drought conditions. Drought tolerance is a very complex trait as it depends not only on the severity of the drought (mild or severe), but also on the developmental stage of the plant as well as the duration. From the physiological point of view, survival is the major aim in plant stress tolerance, whereas from the agricultural point of view crop yield is the trait that determines a drought tolerant crop. This review article highlights the mechanisms and strategies for drought tolerance in fruit crops.

Keywords: Climate change, Abiotic stress, Drought tolerance, Strategies

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Introduction

Globally biotic and abiotic stresses are the serious threat to food security and India will be among the worst affected countries considering its large population under below poverty line. Abiotic stress under the climate change scenario will adversely affect the perennial horticultural crops. Drought and salinity are among the major abiotc stresses that affect 1/3rd global population in terms of human health and farm productivity [1]. Because the world's water supply is limiting, future food demand for rapidly increasing population pressures is likely to further aggravate the effects of drought. Agricultural drought addresses the situation in which the water available to the plants through rainfall and/or irrigation is insufficient to meet the transpiration needs of the crop, which leads to yield reductions [2]. The agricultural drought will differ between crops because of two major factors (crop water demand and crop water supply) [3]. Climatic factors such as high temperature, high wind velocity and low relative humidity are associated with drought. Basically there are two types of drought-atmospheric drought and soil drought. The severity of drought is unpredictable as it depends on many factors such as occurrence and distribution of rainfall, evaporative demands and moisture retaining capacity of soils.

Drought tolerance is a very complex trait as it depends not only on the severity of the drought (mild or severe), but also on the developmental stage of the plant as well as the duration [4, 5]. From the physiological point of view, survival is the major aim in plant stress tolerance, whereas from the agricultural point of view crop yield is the trait that determines a drought tolerant crop [6]. Drought stress causes a wide range of morpho-physiological and biochemical changes that adversely affect the development as well as the productivity of fruit crops.

Effects of drought on fruit crops

The effects of drought range from morphological to molecular levels and are evident at all phenological stages of plant growth at whatever stage the water deficit takes place. Drought restricts water supply which results in a reduction of tissue water content, stomatal conductance, metabolic processes and growth. Numerous studies have shown that plant roots can sense changes in soil water content. As soils become dry, root-sourced signals are

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transported *via* the xylem to leaves and result in reduced water loss and decreased leaf growth. Drought induce numerous morphological, physiological and biochemical changes in all plant organs.

Morphological response

It has been established that drought stress is a very important limiting factor at the initial phase of plant growth and establishment. It affects both elongation and expansion growth [7]. The plant height was reduced up to 25% in water stressed citrus seedlings. Reduces leaf size, stem extension and root proliferation, disturbs plant water relations [8].

Physiological and biochemical response

Closing of the stomata

The first response of virtually all plants to acute water deficit is the closure of their stomata to prevent the transpirational water loss. Drought stress is considered to be a moderate loss of water, which leads to stomatal closure.

Limits gas exchange

Closing of stomata decreases the inflow of CO_2 into the leaves and spares more electrons for the formation of active oxygen species. As the rate of transpiration decreases, the amount of heat that can be dissipated increases.

Photosynthetic activity

A major effect of drought is reduction in photosynthesis, which arises by a decrease in leaf expansion, impaired photosynthetic machinery, premature leaf senescence and associated reduction in food production.

Growth hormone

When exposed to drought stress, plants produce high levels of the hormone abscisic acid (ABA), which induces stomatal closure as well as the expression of various genes. Indeed, it has been shown that exogenous application of ABA can mimic such drought stress responses [9, 10], not all drought stress-induced genes are responsive to exogenous ABA treatment. Endogenous levels of auxins, gibberellins and cytokinin usually decrease, while those of abscisic acid and ethylene increase.

Oxidative damage

Exposure of plants to certain environmental stresses quite often leads to the generation of reactive oxygen species, including superoxide anion radicals (O^{-2}), hydroxyl radicals (OH), hydrogen peroxide, alkoxy radicals (RO) and singlet oxygen (O12). Reactive oxygen species react with proteins, lipids and deoxyribonucleic acid, causing oxidative damage and impairing the normal functions of cells.

Molecular responses

Drought triggers the production of ABA in roots which is transported to the shoots causing stomata closure and eventually restricting growth. Several drought-responsive genes, aquaporins, LEA proteins, heat shock proteins, and dehydrins have been identified.

Mechanism for drought tolerance

Plants adopt to survive under drought stress by the induction of various morphological, biochemical and physiological responses.

Morphological mechanisms

Plant drought tolerance involves changes at whole-plant level. A single or a combination of inherent changes determines the ability of the plant to sustain itself under limited moisture supply. An account of various morphological mechanisms operative under drought conditions is given below [11].

Drought escape

Drought escape is the ability of plants to adjust their growth period or lifecycle to avoid the seasonal drought stress [12].Generally the crop duration is interactively determined by genotype and the environment and determines the ability of the crop to escape from drought. In plants flowering time is an important trait related to drought adaptation, where a short life cycle can lead to drought escape [13]. In field-grown clones of Robusta coffee, leaf shedding in response to drought stress occurred sequentially from older to younger leaves, suggesting that the more drought-sensitive the clone, the greater the extent of leaf shedding [14].



Figure 1 Physiological, biochemical and molecular responses to drought stress in plants [15]

Drought avoidance

Drought avoidance consists of mechanisms that reduce water loss from plants, due to stomatal control of transpiration, and also maintain water uptake through an extensive and prolific root system. A deep and thick root system is helpful for extracting water from considerable depth [16]. Fruit crops like ber, bael, custard apple, phalsa, datepalm, tamarind etc. can be grown in xerophytic conditions.

Phenotypic flexibility

At a morphological level, Plants generally limit the number and area of leaves in response to drought stress just to cut down the water budget at the cost of yield loss. It has long been established that plants bearing small leaves are typical of xeric environments. Such plants withstand drought very well. Leaf pubescence is a xeromorphic trait that helps protect the leaves from excessive heat load. Hairy leaves have reduced leaf temperatures and transpiration [17]. Drought-stressed *Ziziphus* effectively control water loss both through reduction in leaf area and by stomatal closure resulting in higher intrinsic water use efficiency [18].

Physiological mechanisms

Osmotic adjustment, osmoprotection, antioxidation and scavenging defence system are the most important physiological mechanisms responsible for drought tolerance.

Osmotic adjustment

Osmotic adjustment is a mechanism to maintain water relations under osmotic stress. It involves the accumulation of

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soluble solutes like sugars, sugar alcohols, proline, glycinebetaine, organic acids, calcium, potassium, chloride ions etc. [19]. It allows the cell to decrease osmotic potential and, as a consequence, increases the gradient for water influx and maintenance of turgor pressure. Like Osmotic potential of Cherry cultivar 'Colt' and 'Meteor' at full turgor $\Psi_{\pi,sat}$ decreased in response to water stress from leaves and roots [20]. Hexose sugars (particularly glucose have been reported as contributing directly to osmotic adjustment in *Fragaria chiloensis* [21]. This is essential for maintaining physiological activity for extended periods of drought.

Plant growth regulators

Endogenous plant growth regulators play an important role in regulating plant responses to abiotic stress by sensitizing growth and developmental processes. It is documented that the induction in stress tolerance is induced by the manipulations in the concentrations of endogenous PGR under stress conditions by helping plants in many ways. Plant growth regulators *viz*. ABA, brassinosteroids, jasmonate, salicylic acid, polyamines and nitric oxide increase under drought stress [22].

Antioxidant defence system

Enzymes are the most efficient mechanism against oxidative stress. The antioxidant defence system in the plant cell constitutes both enzymatic and non-enzymatic components. Enzymatic components include superoxide dismutase, catalase, peroxidase, ascorbate peroxidase and glutathione reductase. Non-enzymatic components contain cystein, reduced glutathione and ascorbic acid [23]. The reactive oxygen species in plants are removed by a variety of antioxidant enzymes and/or lipid-soluble and water soluble scavenging molecules. The antioxidant enzymes being the most efficient mechanisms against oxidative stress [24].

Drought tolerance strategies

To ensure the productivity and quality of fruits following strategies are used for drought tolerance

Water management

There are mainly two approaches for management of water under drought conditions.

Partial Root zone drying

A new irrigation technique called partial root-zone drying (PRD) was developed in Australia. This technique has been applied successfully in commercial grapevines world-wide in order to reduce vine vigour and water use while maintaining crop yield, and berry size and improving fruit quality compared to conventional irrigation [25]. The concept of PRD allows one part of the root system to dry out while simultaneously the other part is kept wet by frequent irrigation. After a certain period of time, around 5-14 days, depending on soil and climatic conditions, the irrigation is switched so that the former 'wet' part of the root system is allowed to dry out and the former 'dry' part is irrigated. Dehydrating roots send chemical signals, such as abscisic acid (ABA), to the shoots and leaves via the xylem, reducing stomatal conductance, transpiration, and vegetative growth. Meanwhile, roots of the watered side maintain a favourable plant water status. This irrigation technique has also increased considerably water use efficiency in grapevines, by up to 50% or more compared to conventional irrigation.

Regulated deficit irrigation (RDI)

Regulated deficit Irrigation is an irrigation scheduling technique originally developed for pome and stone fruit orchards, has been adapted successfully for wine grape production. Water deficit is applied during the post-set period of berry development to reduce vegetative growth and, as necessary, berry size of red-wine grape varieties. However, water deficit is avoided during the berry-ripening period, and precise irrigation management is required to ensure minimal competition between ripening berries and vegetative growth. For the variety Shiraz, in particular, this irrigation practice has resulted in significant improvements in wine quality. Both PRD and RDI systems require high management skills, and accurate monitoring of soil water content is recommended. Drip and other forms of micro-irrigation facilitate the application of RDI and PDR.

Soil moisture conservation

Technique like mulching, basin listing, compartmental bunding *etc*. can be utilized to conserve soil moisture. Mulching either with black polythene or locally available mulch helps in reducing the evaporation.

Selection of fruit crops

They should possess drought tolerance mechanism like deep root system (ber, datepalm), leaf shedding (ber, gonda), water binding mechanism (fig), presence of thorn (karonda), leaf orientation (aonla) and well formed canopy (kinnow).

Selection of varieties

Varieties for drought conditions should be short in duration. Some of the drought tolerant varieties in fruit crop *viz.* – Ruby (Pomegranate), Arka Sahan (Annona), Deanna and Excel (Fig) and Banana- cultivars belonging to BB genome shown to be drought tolerant *viz.* Karpuravalli and Kanthali [26].

Application of PGR

Application of Paclobutrazol (10 mg/l) is used to avoid moisture stress in mango and exogenous application of jasmonic acid induced drought tolerance by increasing the betaine level in pear [27].

Mycorrhizal association

Arbuscular mycorrhizal fungus (AMF) induced drought tolerance in *Citrus* species. Genera such as *Acaulospora*, *Gigaspora*, and *Glomus* were dominantly observed in the citrus rhizosphere [28]. AMF inoculation with *Glomus mosseae* significantly increased the active and total absorption areas of root systems in the Trifoliate Orange seedlings grown at varying soil water contents compared to non-AM inoculation [29].

Rootstock

One of the strategies to improve fruit tree response to water deficit conditions is the use of tolerant rootstock genotypes. The use of drought tolerant rootstocks would minimise the immediate effects of dry conditions and enable the variety to recover quickly. With increased awareness about the use of rootstocks in overcoming the adverse effects of drought growers started using rootstock for the cultivation [30].

Table 1 Drought tolerant rootstocks in fruit crops [31].			
Sr. No.	Crop	Drought tolerant rootstock	
1	Almond	Prunus xerophila, P. amygdaliformis and P. Elaeagrifolia	
2	Ber	Zizyphus nummularia and Zizyphus lotus	
3	Apple	MM111	
4	Grape	110R and Dogridge	
5	Pear	Pyrus betulaefolia and Pyrus calleryan	

Transgenic Approach

The plant growth and productivity of many crops are adversely affected by drought. Transgenic approach is now a widely used procedure for introducing genes from distant genepools, ranging from prokaryotic organisms such as *E. coli* to halophytes or glycophytes, into many plant species for the development of stress tolerant plants [32]. Genetic engineering for improved abiotic stress-tolerance by expressing transcription factors has been achieved in a number of fruit plants. For instance, encoding a transcription factor belonging to the *Myb* family was able to improve tolerance to cold and drought stress in transgenic apple through improved physiological and biochemical adaptation [33]. Transgenic apple ('Royal Gala') plants overexpressing a cytosolic APX (ascorbate peroxidase) gene have indicated an increased tolerance to stress [34]. Introduction of p5cs gene in the citrus rootstock Carrizo Citrange conferred higher accumulation of proline in leaves [35].

Conclusion

Drought stress is one of the most ominous abiotic factor limiting the productivity and quality of fruit crops resulting in huge economic loss to the fruit growers. It induces stomatal closure, decreases transpiration and photosynthetic rates, and leads to poor productivity. To minimize the negative effects of water stress, plants have various signalling pathways and respond by changing their growth pattern, up-regulation of antioxidants, accumulation of compatible solutes and by producing stress proteins. The drought tolerance is a complex mechanism involves a number of processes at cell, tissue, organ and whole-plant levels, when activated at different stages of plant development. Drought stress effects can be managed by developing drought resistant genotypes, plant growth regulators, use of osmoprotectants, and some other strategies. Applications of genomics, proteomics and trascriptomic approaches to a better understanding of the molecular basis of plant drought tolerance and improved water-use efficiency under drought are also imperative. Molecular knowledge of response and tolerance mechanisms is likely to pave the way for engineering plants that can withstand and give satisfactory economic yield under drought stress.

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