

A review: Morphological, physiological, biochemical and molecular plant responses to water deficit stress

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ABSTRACT

In the conditions of changing climate, plants are continuously subject to several biotic and abiotic stresses. Among these stresses, drought is one of the most severe abiotic stress which threatens crops production and yield. Crops demonstrate various morphological, physiological, biochemical and molecular responses under water stress. This review describes some aspects of drought induced changes in morphological, physiological, biochemical and molecular changes in plants. Drought triggers a wide variety of plant responses, ranging from cellular metabolism to changes in growth development including roots, shoots and final yield. Moreover, understanding the biochemical and molecular responses to drought is essential for perception of plant resistance mechanisms to water-limited conditions. The sections of this review deal with plant responses including root growth, transpiration, photosynthesis, phenotypical flexibility, accumulation of solutes and expression of some genes and proteins for improving the tolerance to the drought stress.

Keywords: adaptation, drought, yield

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I. INTRODUCTION

Crop yield reduction, as a consequence of increasingly severe climatic change, threatens food security. Plant growth is highly influenced by environmental stresses. Resistance to stresses is a complex task which make difficult to find an observable genetic correlation between a morphological, physiological traits and yield performance under field conditions. Abiotic stresses, including water deficit, salinity and extreme temperatures, are the most important to be considered in the selection of new genotypes because it affects crop production. Among these stress, drought is one of the most adverse factors of plant growth and productivity [1]. There are different types of plant reactions to this stress: (i) stress escape (ii) stress avoidance; and (iii) stress tolerance. Drought stress is a very complex character depending on severity, duration of the stress event, and the plant growth stage. Plant drought tolerance involves changes at whole-plant functions. For these reasons, it is necessary to determine the most suitable conditions in which to observe the type of response that is better in order to improve plant performance. Water stress induces many physiological, biochemical and molecular response on plants. Moderate to severe water stress affects various morpho-physiological traits such as chlorophyll fluorescence, water use efficiency and dry matter yield, water content and water potential membrane stability [2,3]and pigment content stability [4,5,6]. Drought stress progressively reduces CO₂ assimilation rates owing to decrease stomatal conductance. It affects leaf size, stems extension and root proliferation, troubles plant water relations and decreases water-use efficiency. It disrupts photosynthetic pigments and reduces the gas exchange and the production of active oxygen species causes a decrease in plant growth and productivity. This review focuses on the ability and strategies of plants to respond and adapt to drought stress.

II. AGRO-MORPHOLOGICAL PLANT RESPONSE TO DROUGHT STRESS

Drought stress is an important environmental limiting factor at the juvenile stage of plant growth and establishment. In fact, seed germination is the first stage of growth that is sensitive to water deficit. Therefore, germination of seeds, vigour and coleoptile length are crucials for the establishment of plants. Visible syndromes of plant subject to water deficit in the vegetative phase are leaf wilting, a decrease in plant height, number and area of leaves and delay in formation of buds and flowers [7]. In fact, limitation of leaf growth is among the earliest visible impacts of water stress because leaves determine radiation interception and are the main photosynthetic organs [8]. Water deficit stress mostly reduced leaf water potential and growth and in turn the leaf areas in many species and leaf senescence could be observed under severe water stress [9, 10, 11]. In

fact, development of optimal leaf area is important to photosynthesis and dry matter yield. According to Lonbani and Arzani [12], leaf extension can be reduced under drought environment in order to get a balance between the water status of plant tissues and the water absorbed by plant roots [13]. In addition, Blum [14] suggested that a small leaf area is beneficial under drought stress in order to avoid hydration. Moreover, water availability is preliminary sensed by roots affects roots growth and root system architecture (root length, spread, number, and length of lateral roots) [15, 16]. Roots are essential for plant functions and productivity, such as water and nutrient uptake, forming symbioses with other microorganisms in the rhizosphere. Thus, a prolific root system can confer the advantage to support accelerated plant growth during the early crop growth stage and extract water from soil [17]. Drought stress reduced the number of days to heading, peduncle length and plant fresh and dry biomass production [10, 18]. Peduncle length has been also suggested as useful indicator of yield performance in stress conditions. Kaya et al. [19] have been found a positive correlation between peduncle length and grain yield. Water stress affects also yield and its related traits such as number of spike per m², grain per spike number, 1000 grain weight and grain weight per spike particularly in arid and semi-arid regions [20]. The effect of deficit water on yield and its yield components at different growth stages have been noted by several authors [21]. In fact, drought stress may occur throughout the growing season, early or late season, yield is reduced mostly when water stress occurs during the heading or flowering phases but its effect on yield reduction is highest when it occurs after anthesis. Drought stress can reduce 17 to 70% of grain yield in the case of the durum wheat [22]. During maturity, this stress resulted in about 10% decrease in yield but moderate stress during the early vegetative growth has mainly no effect on yield [23].

III. PHYSIOLOGICAL PLANT RESPONSE TO WATER STRESS

The mainly effect of drought is limiting photosynthesis through stomatal closure which limits CO₂ uptake by leaves and prevent the transpirational water loss as result to the reduction in leaf turgor and/or water potential [24, 25]. The limitation CO₂ availability causes the photo-damage [26]. Drought stress suppress particularly photochemical efficiency of photosystem PS II by decreasing electron transport, removal of external proteins, and release of calcium and magnesium ions from their binding [27, 28]. Very severe drought conditions reduce photosynthesis due to a decrease in Rubisco activity [29]. The activity of the photosynthetic electron transport chain is finely tuned to the presence of CO₂ in the chloroplast and change in photosystem II under drought conditions. Drought stress produced changes in the ratio of chlorophyll 'a' and 'b' and carotenoids [10]. Chlorophyll concentration has considered as an index for evaluation of source. In fact, resistant cultivar to water stress had high chlorophyll content [30]. In this context, Ashraf et al. [31] found that drought stress reduced concentration of chlorophyll b more than chlorophyll a.

Water stress causes also the reduction of relative water content [32, 33]. In fact, high relative water content is a resistant mechanism to drought and is related to more osmotic regulation or less elasticity of tissue cell wall [34]. The osmotic adjustment is the process of accumulation of solutes in response to water stress by maintaining turgor in tissues. Solute accumulation contributed to osmotic adjustment in plants, include inorganic cations, organic acids, carbohydrates and free amino acids. In some plants potassium is the primary inorganic cation accumulating during water stress and it is often the most abundant solute in leaf [35, 36].

Osmotic adjustment depends highly on photosynthesis to supply compatible solute. As dehydration becomes more severe, photosynthesis is inhibited, resulting in smaller solute supply for osmotic adjustment. With continued water limitation, osmotic adjustment delays, but cannot completely prevent, dehydration [37]. Osmotic adjustment is not permanent and plants often respond rapidly to reduce presence of water. Osmoregulation and turgor maintenance permit continued root growth and efficient uptake of soil moisture [38]. However, despite the accumulation of ions and organic solutes, allowing osmotic adjustment in the meristematic and expanding regions, growth of the shoot may still be inhibited by stress, either because osmotic adjustment may not be sufficiently rapid to compensate for growth or due to a stress induced fall in turgor.

IV. BIOCHEMICAL DERIVATIONS OF DROUGHT TOLERANCE

Drought induces important alterations in plant biochemistry and metabolism. Under drought stress, the responses deal with the production of reactive oxygen species (ROS) which cause membrane injuries, protein degradation, enzyme inactivation and thus induce oxidative stress [39].

Under water deficit conditions, the accumulation of ABA hormone plays a great role in response and tolerance to dehydration. Closure of stomata and induction of the expression of multiple genes involved in defense against the drought stress are functions of ABA. The amount of ABAs in xylem saps increases substantially under reduced water availability in the soil, and this results in an increased ABA concentration in different compartments of the leaf. Another well-known effect of drought in plants is the decrease in PM-ATPase activity. Low PM-ATPase increases the cell wall pH and lead to the formation of ABA- form of abscisic acid. ABA- cannot penetrate the plasma membrane and translocate toward the guard cell by the water stream in the leaf apoplast. High ABA concentration around guard cell results in stomata closure and help to keep water.

Under water stress conditions, plants synthesize alcohols, sugars, proline, glycine, betaine and putrescine and accumulate solutes [40, 41]. Dehydrins have been the most observed group among the accumulated proteins in response to loss of water and increased in barley and maize under water stress. LEA proteins play an important role as protection of plants. Osmotin is also an accumulated protein under water stress in several plant species such as tobacco, triplex, tomato and maize [42]. Moreover, accumulation of proline in plant tissues is considered as an indicator of tolerance to drought stress. In this context, it is reported that proline content in resistant wheat cultivars was more than in sensitive cultivar under the drought stress. Soluble carbohydrates accumulation has also a role in osmotic regulations and conservation mechanism [43]. Lipids, one of the major components of plant membrane, are affected by water stress. In plant cell, polar acyl lipids are the main lipids associated with membrane structures [44]. Glycolipids (GL) are found in chloroplast membranes (more than 60%) and phospholipids (PL) are thought to be the most important mitochondrial and plasma membrane lipids [45].

V. MOLECULAR RESPONSES

The understanding of molecular responses of plants to abiotic stresses involved the development of new tools via genetic manipulation by expression of several stress induced genes. A number of different types of proteins are likely to function to improve stress tolerance. Genes encoding the enzymes of osmolyte biosynthesis permit the synthesis of these osmotic compounds in response to stress. Proline is synthesized from L-glutamic acid through D1-pyrroline-5-carboxylate (P5C) by two enzymes: P5C synthetase and P5C reductase. Proline dehydrogenase and P5C dehydrogenase are the enzymes that degrade proline to L-glutamic acid. In response to water deficit, P5C synthetase is induced and proline dehydrogenase is repressed, resulting in a net accumulation of proline. Another class of genes, which may be unique to plants, is induced in plants subjected to water deficit. These genes called the late embryogenesis abundant genes, abbreviated as lea genes, are also developmentally programmed for expression in desiccating seeds. These genes encode small hydrophilic proteins that are predicted to protect proteins and membranes when cellular dehydration occurs. In the case of wheat, there are several genes which are responsible for drought stress tolerance and produce different types of enzymes and proteins for instance, late embryogenesis abundant (lea), responsive to abscisic acid (Rab), rubisco, helicase, proline, glutathione-S-transferase (GST), and carbohydrates during drought stress [46].

In this approach the simultaneous analysis of a great number of genes is possible, and all the studies based on data indicating that several genes are involved in the modulation of plant adaptation to environmental stresses. However, there is the need to further analyze plant stress response at molecular level due to the complexity of events associated with the sensing of stress and the activation of specific pathways. This complexity is even greater when a combination of different stresses such as heat and drought is simultaneously applied.

VI. CONCLUSION

Water deficit affects the development, growth and yield in plant crop, but the tolerance crops to this stress varies remarkably. Changes in morphological, physiological, biochemical and molecular aspects are generally noted in response to drought stress. Understanding these responses to drought is important for screening tolerance of genotypes to water-limited conditions.

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