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Review article

Plant drought stress: effects, mechanisms and management

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Abstract – Scarcity of water is a severe environmental constraint to plant productivity. Drought-induced loss in crop yield probably exceeds losses from all other causes, since both the severity and duration of the stress are critical. Here, we have reviewed the effects of drought stress on the growth, phenology, water and nutrient relations, photosynthesis, assimilate partitioning, and respiration in plants. This article also describes the mechanism of drought resistance in plants on a morphological, physiological and molecular basis. Various management strategies have been proposed to cope with drought stress. Drought stress reduces leaf size, stem extension and root proliferation, disturbs plant water relations and reduces water-use efficiency. Plants display a variety of physiological and biochemical responses at cellular and whole-organism levels towards prevailing drought stress, thus making it a complex phenomenon. CO_2 assimilation by leaves is reduced mainly by stomatal closure, membrane damage and disturbed activity of various enzymes, especially those of CO_2 fixation and adenosine triphosphate synthesis. Enhanced metabolite flux through the photorespiratory pathway increases the oxidative load on the tissues as both processes generate reactive oxygen species. Injury caused by reactive oxygen species to biological macromolecules under drought stress is among the major deterrents to growth. Plants display a range of mechanisms to withstand drought stress. The major mechanisms include curtailed water loss by increased diffusive resistance, enhanced water uptake with prolific and deep root systems and its efficient use, and smaller and succulent leaves to reduce the transpirational loss. Among the nutrients, potassium ions help in osmotic adjustment; silicon increases root endodermal silicification and improves the cell water balance. Low-molecular-weight osmolytes, including glycinebetaine, proline and other amino acids, organic acids, and polyols, are crucial to sustain cellular functions under drought. Plant growth substances such as salicylic acid, auxins, gibberrellins, cytokinin and abscisic acid modulate the plant responses towards drought. Polyamines, citrulline and several enzymes act as antioxidants and reduce the adverse effects of water deficit. At molecular levels several drought-responsive genes and transcription factors have been identified, such as the dehydration-responsive element-binding gene, aquaporin, late embryogenesis abundant proteins and dehydrins. Plant drought tolerance can be managed by adopting strategies such as mass screening and breeding, marker-assisted selection and exogenous application of hormones and osmoprotectants to seed or growing plants, as well as engineering for drought resistance.

drought response / stomatal oscillation / osmoprotectants / hormones / stress proteins / drought management / CO_2

1. INTRODUCTION

Faced with scarcity of water resources, drought is the single most critical threat to world food security. It was the catalyst of the great famines of the past. 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 (Somerville and Briscoe, 2001). The severity of drought is unpredictable as it depends on many factors such as occurrence and distribution of rainfall, evaporative demands and moisture storing capacity of soils (Wery et al., 1994).

Investigations carried out in the past provide considerable insights into the mechanism of drought tolerance in plants at molecular level (Hasegawa et al., 2000). Three main mechanisms reduce crop yield by soil water deficit: (i) reduced canopy absorption of photosynthetically active radiation, (ii) decreased radiation-use efficiency and (iii) reduced harvest index (Earl and Davis, 2003). The reproducibility of drought stress treatments is very cumbersome, which significantly impedes research on plant drought tolerance. A slow pace in revealing drought tolerance mechanisms has hampered both traditional breeding efforts and use of modern genetics approaches in the improvement of drought tolerance of crop plants (Xiong et al., 2006). Although plant responses to drought are relatively well known, plant performance under a more complex environment where multiple stresses co-occur is fragmentary. That is why the plants have to respond

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simultaneously to multiple stresses, e.g. drought, excessive light and heat, which may coincide in the field. These kinds of investigations are usually not predictable from single factor studies (Zhou et al., 2007).

It is imperative to improve the drought tolerance of crops under the changing circumstances. Currently, there are no economically viable technological means to facilitate crop production under drought. However, development of crop plants tolerant to drought stress might be a promising approach, which helps in meeting the food demands. Development of crops for enhanced drought resistance, among other things, requires the knowledge of physiological mechanisms and genetic control of the contributing traits at different plant developmental stages. Valuable work has been done on drought tolerance in plants. Ingram and Bartels (1996) more than a decade ago elegantly reviewed those appreciable efforts. More recent reviews deal with specific aspects of plant drought tolerance (Penna, 2003; Reddy et al., 2004; Agarwal et al., 2006). This review encompasses an overview of the current work reported on some effects and mechanisms of drought tolerance in higher plants and important management strategies to overcome the drought effects, mainly on field crops.

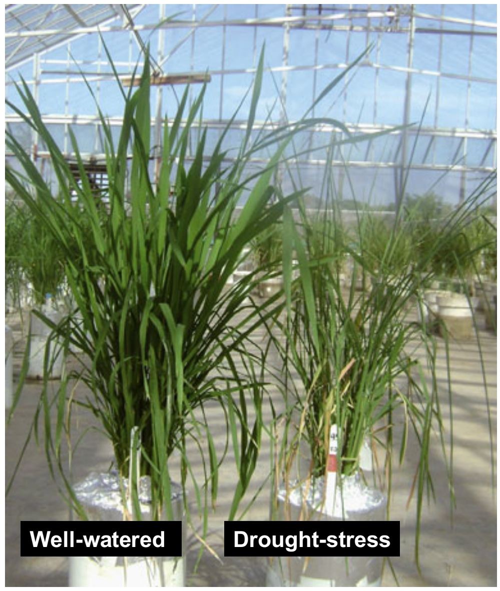

Figure 1. Effect of drought stress on the vegetative growth of rice cv. IR64. Both the plants were grown under well-watered conditions up to 20 days following emergence. One pot was submitted to progressive soil drying (drought stress). The afternoon before the drought, all pots were fully watered (to saturation). After draining overnight, the pots were enclosed around the stem to prevent direct soil evaporation. A small tube was inserted for re-watering pots. The decrease in soil moisture was controlled by partial re-watering of the stressed pots to avoid a quicker imposition of stress and to homogenize the development of drought stress. A well-watered control pot was maintained at the initial target weight by adding the daily water loss back to the pot. This figure shows the plants 20 days after imposition of drought stress.

2. EFFECTS OF DROUGHT ON PLANTS

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. An account of various drought stress effects and their extent is elaborated below.

2.1. Crop growth and yield

The first and foremost effect of drought is impaired germination and poor stand establishment (Harris et al., 2002). Drought stress has been reported to severely reduce germination and seedling stand (Kaya et al., 2006). In a study on pea, drought stress impaired the germination and early seedling growth of five cultivars tested (Okcu et al., 2005). Moreover, in alfalfa (*Medicago sativa*), germination potential, hypocotyl length, and shoot and root fresh and dry weights were reduced by polyethylene glycol-induced water deficit, while the root length was increased (Zeid and Shedeed, 2006). However, in rice, drought stress during the vegetative stage greatly reduced the plant growth and development (Fig. 1; Tripathy et al., 2000; Manikavelu et al., 2006).

Growth is accomplished through cell division, cell enlargement and differentiation, and involves genetic, physiological, ecological and morphological events and their complex interactions. The quality and quantity of plant growth depend on these events, which are affected by water deficit (Fig. 2). Cell growth is one of the most drought-sensitive physiological processes due to the reduction in turgor pressure (Taiz and Zeiger, 2006). Under severe 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).

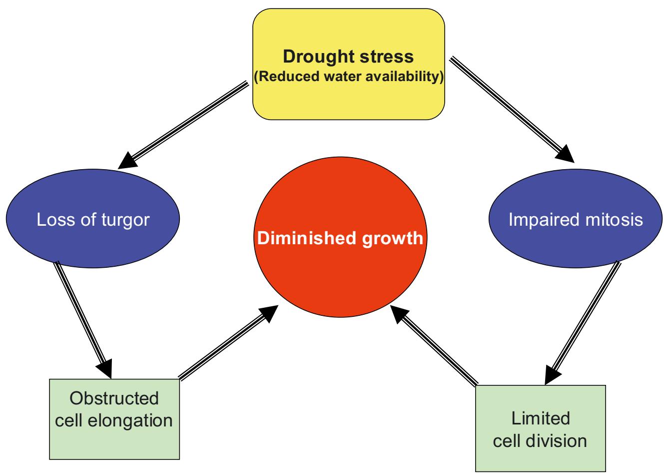

Figure 2. Description of possible mechanisms of growth reduction under drought stress. Under drought stress conditions, cell elongation in higher plants is inhibited by reduced turgor pressure. Reduced water uptake results in a decrease in tissue water contents. As a result, turgor is lost. Likewise, drought stress also trims down the photo-assimilation and metabolites required for cell division. As a consequence, impaired mitosis, cell elongation and expansion result in reduced growth.