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Effects of Drought on Crop Yield Potential

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Abstract

Drought is a recurrent feature of the climate, varying in intensity, duration, and frequency across the climatic spectrum. A drought can have substantial economic, environmental, and social impacts. Drought is a weather-related natural disaster. It affects vast regions for months or years. It has an impact on food production and it reduces life expectancy and the economic performance of large regions or entire countries. Conventional plant breeding attempts have changed over to use physiological selection criteria since they are time consuming and rely on present genetic variability. Tolerance to abiotic stresses is very complex, due to the intricate of interactions between stress factors and various molecular, biochemical and physiological phenomena affecting plant growth and development. High yield potential under drought stress is the target of crop breeding. In many cases, high yield potential can contribute to yield in moderate stress environment.

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Stress; natural disaster; Tolerance; scarcity

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 in 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. Therefore, the objective of this review paper was: - to understand and know the ways of developing crop varieties which are tolerable to drought and gives adequate yield.

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.

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).

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. 1). 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).

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.

Water relations

Relative water content, leaf water potential, stomatal resistance, rate of transpiration, leaf temperature and canopy temperature are important characteristics that influence plant water relations. Relative water content of wheat leaves was higher initially during leaf development and decreased as the dry matter accumulated and leaf matured (Siddique *et al.*, 2001). Obviously, water-stressed wheat and rice plants had lower relative water content than non-stressed ones. Exposure of these plants to drought stress substantially decreased the leaf water potential, relative water content and transpiration rate, with a concomitant increase in leaf temperature (Siddique *et al.*, 2001).

The ratio between dry matter produced and water consumed is termed as water-use efficiency at the whole-plantlevel (Monclus *et al.*, 2005). Abbate *et al.*, (2004) concluded that under limited supply, water-use efficiency of wheat was greater than in well-watered conditions.

They correlated this higher water-use efficiency with stomatal closure to reduce the transpiration. In another study on clover (*Trifolium alexandrinum*), water-use efficiency was increased due to lowered water loss under drought stress, primarily by decreased transpiration rate and leaf area, and relatively lesser reduction in yield (Lazaridou and Koutroubas, 2004).

In fact, although components of plant water relations are affected by reduced availability of water, stomatal opening and closing is more strongly affected. Moreover, change in leaf temperaturemay be an important factor in controlling leaf water status under drought stress. Drought-tolerant species maintain water-use efficiency by reducing the water loss. However, in the events where plant growth was hindered to a greater extent, water-use efficiency was also reduced significantly.

Nutrient relations

Decreasing water availability under drought generally results in limited total nutrient uptake and their diminished tissue concentrations in crop plants. An important effect of water deficit is on the acquisition of nutrients by the root and their transport to shoots. Lowered absorption of the inorganic nutrients can result from interference in nutrient uptake and the unloading mechanism, and reduced transpirational flow (Garg, 2003; McWilliams, 2003). However, plant species and genotypes of a species may vary in their response to mineral uptake under water stress. In general, moisture stress induces an increase in N, a definitive decline in P and no definitive effects on K (Garg, 2003).

Transpiration is inhibited by drought, as shown for beech (Peuke *et al.*, 2002), but this may not necessarily affect nutrient uptake in a similar manner. Influence of drought on plant nutrition may also be related to limited availability of energy for assimilation of NO$^{-\ 3}$ /NH^{+4}, PO3$^{-\ 4}$ and SO2$^{-\ 4}$: they must be converted in energy-dependent processes before these ions can be used for growth and development of plants (Grossman and Takahashi, 2001).

Photosynthesis

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 (Wahid and Rasul, 2005).

When stomatal and non-stomatal limitations to photosynthesis are compared, the former can be quite small. This implies that other processes besides CO2 uptake are being damaged.

The role of drought-induced stomatal closure, which limits CO2 uptake by leaves, is very important. In such events, restricted CO2 availability could possibly lead to increased susceptibility to photo-damage (Cornic and Massacci, 1996).

Drought stress produced changes in photosynthetic pigments and components (Anjum *et al.*, 2003), damaged photosynthetic apparatus (Fu J. and Huang, 2001) and diminished activities of Calvin cycle enzymes, which are important causes of reduced crop yield (Monakhova and Chernyadèv, 2002).

Another important effect that inhibits the growth and photosynthetic abilities of plants is the loss of balance between the production of reactive oxygen species and the antioxidant defense (Fu J. and Huang, 2001; Reddy *et al.*, 2004), causing accumulation of reactive oxygen species which induces oxidative stress in proteins, membrane lipids and other cellular components. Some important components of photosynthesis affected by drought are discussed below.

Stomatal oscillations

The first response of virtually all plants to acute water deficit is the closure of their stomata to prevent the transpirational water loss (Mansfield and Atkinson, 1990). This may result in response to either a decrease in leaf turgor and/or water potential (Ludlow and Muchow, 1990) or to a low-humidity atmosphere (Maroco *et al.*, 1997).

Photosynthetic enzymes

Very severe drought conditions limit photosynthesis due to a decline in Rubisco activity (Bota *et al.*, 2004). The activity of the photosynthetic electron transport chain is finely tuned to the availability of CO2 in the chloroplast and change in photosystem II under drought conditions (Loreto *et al.*, 1995). Dehydration results in cell shrinkage, and consequently a decline in cellular volume. This makes cellular contents more viscous.

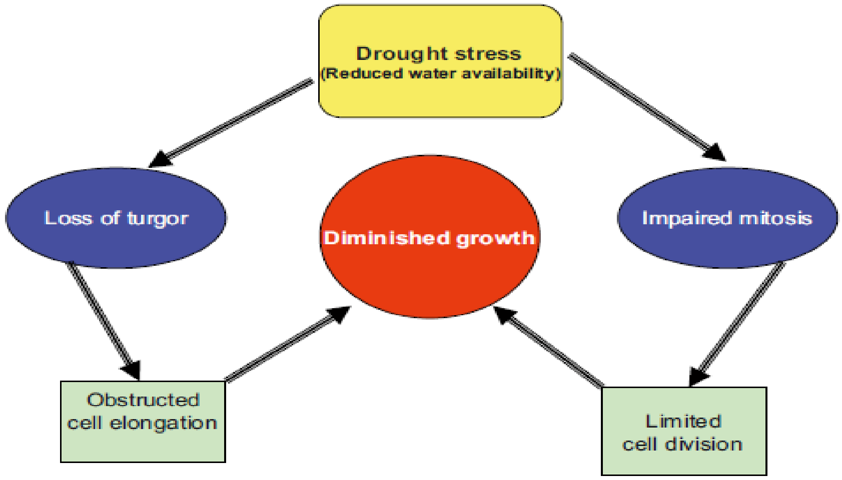
Therefore, an increase in the probability of protein-protein interaction leads to their aggregation and denaturation (Hoekstra *et al.*, 2001). Increased concentration of solutes, leading to increased viscosity of the cytoplasm, may become toxic and may be deleterious to the functioning of enzymes, including those of the photosynthetic machinery (Hoekstra *et al.*, 2001).

Adenosine triphosphate synthesis

There is a long-standing controversy as to whether drought mainly limits photosynthesis through stomatal closure (Cornic and Massacci, 1996) or by metabolic impairment (Tezara *et al.*, 1999). Evidence that impaired adenosine triphosphate synthesis is the main factor limiting photosynthesis even under mild drought has further stimulated the debate (Lawlor and Cornic, 2002). It is reported that impaired photophosphorylation and adenosine triphosphate synthesis are the main factors limiting photosynthesis even under mild drought (Tezara *et al.*, 1999).

Under drought stress, production of limited nicotinamide adenine dinucleotide phosphate maintains the continuation of electron transport, although the status of the reductant may be high even when the fluxes are small, leading to a more increased demand than supply. Under drought stress, non-cyclic electron transport is down-regulated to match the requirements of decreased nicotinamide adenine dinucleotide phosphate production and cyclic electron transport is activated.

Fig.1 Description of possible mechanisms of growth reduction under drought stress



This generates a proton gradient that induces the protective process of high-energy-state quenching (Golding and Johnson, 2003).

Assimilate partitioning

Assimilate translocation to reproductive sinks is vital for seed development. Seed set and filling can be limited by availability or utilization, i.e., assimilate source or sink limitation, respectively (Asch *et al.,* 2005). Drought stress frequently enhances allocation of dry matter to the roots, which enhance water uptake (Leport *et al.*, 2006). De Souza and Da Silv (1987), while analyzing the partitioning and distribution of photo-assimilates in annual and perennial cotton under drought stress, reported that the root-to-shoot dry matter ratio was high in perennial cotton, thereby showing a preferential accumulation of starch and dry matter in roots as an adaptation to drought. Thus, perennial cotton apparently owed its drought resistance to the partitioning of assimilates that favored starch accumulation and growth of the root system. The export rate of sucrose from source to sink organs depends upon the current photosynthetic rate and the concentration of sucrose in the leaves (Komor, 2000). Drought stress decreases the photosynthetic rate, and disrupts the carbohydrate metabolism and level of sucrose in leaves that spills over to a decreased export rate.

This is presumably due to drought stress-induced increased activity of acid invertase (Kim *et al.*, 2000). Limited photosynthesis and sucrose accumulation in the leaves may hamper the rate of sucrose export to the sink organs and ultimately affect the reproductive development. Apart from source limitation, the capacity of the reproductive sinks to utilize the incoming assimilates is also affected under drought stress.

Respiration

Drought tolerance is a cost-intensive phenomenon, as a considerable quantity of energy is spent to cope with it. The fraction of carbohydrate that is lost through respiration determines the overall metabolic efficiency of the plant (Davidson *et al.*, 2000). The root is a major consumer of carbon fixed in photosynthesis and uses it for growth and maintenance, as well as dry matter production (Lambers *et al.,* 1996). Plant growth and developmental processes as well as environmental conditions affect the size of this fraction (i.e. utilized in respiration). However, the rate of photosynthesis often limits plant growth when soil water availability is reduced (Huang and Fu, 2000). A negative carbon balance can occur as a result of diminished photosynthetic capacity during drought, unless simultaneous and proportionate reductions in growth and carbon consumption take place.

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 (H2O2), alkoxy radicals (RO) and singlet oxygen (O12) (Munné-Bosch and Penuelas, 2003). Reactive oxygen species may react with proteins, lipids and deoxyribonucleic acid, causing oxidative damage and impairing the normal functions of cells (Foyer and Fletcher, 2001). Many cell compartments produce reactive oxygen species; of these, chloroplasts are a potentially important source because excited pigments in thylakoid membranes may interact with O^2 to form strong oxidants such as O^{-2} or O12 (Niyogi, 1999; Reddy *et al.*, 2004). Further downstream reactions produce other reactive oxygen species such as H2O2 and OH^-. The interaction of O^2 with reduced components of the electron transport chain in mitochondria can lead to reactive oxygen species formation (Möller, 2001), and peroxisomes produce H2O2 when glycolate is oxidized into glyoxylic acid during photorespiration (Fazeli *et al.*, 2007).

Drought stress is considered to be a moderate loss of water, which leads to stomata closure and limitation of gas exchange. Desiccation is much more extensive loss of water, which can potentially lead to gross disruption of metabolism and cell structure and eventually to the cessation of enzyme catalyzed reactions. Drought stress is characterized by reduction of water content, diminished leaf water potential and turgor loss, closure of stomata and decrease in cell enlargement and growth. Severe water stress may result in the arrest of photosynthesis, disturbance of metabolism and finally the death of plant. It reduces plant growth by affecting various physiological and biochemical processes, such as photosynthesis, respiration, translocation, ion uptake, carbohydrates, nutrient metabolism and growth promoters.

Drought is considered the single most devastating environmental stress, which decreases crop productivity more than any other environmental stress. Impacts are commonly referred to as direct and indirect. Direct impacts include reduced crop, rangeland, and forest productivity, increased fire hazard, reduced water levels, increased livestock and wildlife mortality rates, and damage to wildlife and fish habitat. Impact assessment is carried out on the basis of land-use type, persistence of stressed conditions, demographics and existing infrastructure, intensity and areal extent, and its effect on agricultural yield, public health, water quantity and quality, and building subsidence.

Response includes improved drought monitoring, better water and crop management, augmentation of water supplies with groundwater, increased public awareness and education, intensified watershed and local planning, reduction in water demand, and water conservation. One ideal approach for avoiding the drought symptoms induced by inadequate rainfall is to utilize water reserves to provide supplementary crop irrigation.

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