

Chapter 1

Drought Stress in Plants: An Overview

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Abstract Drought is one of the major constraints limiting crop production worldwide. Crop growth models predict that this issue will be more severe in future. Drought impairs normal growth, disturbs water relations, and reduces water use efficiency in plants. Plants, however, have a variety of physiological and biochemical responses at cellular and whole organism levels, making it a more complex phenomenon. The rate of photosynthesis is reduced mainly by stomatal closure, membrane damage, and disturbed activity of various enzymes, especially those involved in ATP synthesis. Plants display a range of mechanisms to withstand drought, such as reduced water loss by increased diffusive resistance,

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increased water uptake with prolific and deep root systems, and smaller and succulent leaves to reduce transpirational loss. Low-molecular-weight osmolytes, including glycinebetaine, proline and other amino acids, organic acids, and polyols also play vital roles in sustaining cellular functions under drought. Plant growth substances such as salicylic acid, auxins, gibberellins, cytokinins, and abscisic acid modulate plant responses toward drought. Polyamines, citrulline, and several enzymes act as antioxidants and reduce adverse effects of water deficit. Plant drought stress can be managed by adopting strategies such as mass screening and breeding, marker-assisted selection, and exogenous application of hormones and osmoprotectants to seeds or growing plants, as well as engineering for drought resistance. Here, we provide an overview of plant drought stress, its effects on plants' resistance mechanisms and management strategies to cope with drought stress.

Abbreviations

ABA	Abscisic acid
ADC2	Arginine decarboxylase 2 gene
A_{\max}	Maximum photosynthetic efficiency
APX	Ascorbate peroxidase
BRs	Brassinolides
CAT	Catalase
chl	Chlorophyll
Cks	Cytokinins
DRE/CRT	Dehydration-responsive element/C-repeat
DREB	Dehydration-responsive element binding proteins
EBR	Epibrassinolide
ETC	Electron transport chain
GA ₃	Gibberellins
GB	Glycinebetaine
GR	Glutathione reductase
H ⁺ -ATPase	Hydrogen pump ATPase protein
H ₂ O ₂	Hydrogen peroxide
IAA	Indole acetic acid
K	Potassium
LAI	Leaf area index
LEA	Late embryogenesis abundant
N	Nitrogen
O ₂ ⁻	Superoxide radicals
O ₂ ¹	Single oxygen
OH ⁻	Hydroxyl radicals
OsRDCPs	<i>Oryza sativa</i> RING domain-containing proteins
P	Phosphorous
PA	Polyamine
PAL	Phenylalanine ammonia-lyase

POX	Peroxidase
PPO	Polyphenol oxidase
PSI	Photosystem I
PSII	Photosystem II
QTL	Quantitative trait loci
RO	Alkoxy radicals
ROS	Reactive oxygen species
Rubisco	Ribulose-1,5-bisphosphate carboxylase/oxygenase
RuBP	Ribulose-1,5-bisphosphate
RWC	Relative water contents
SA	Salicylic acid
Si	Silicon
SOD	Superoxide dismutase
TcADC	Arginine decarboxylase
TcODC	Ornithine decarboxylase
TcSAMDC	S-adenosylmethionine decarboxylase
TcSPDS	Spermidine synthase
TcSPMS	Spermine synthase
$V_{c,max}$	Carboxylation velocity of Rubisco
WUE	Water use efficiency

1.1 Introduction

Crop plants are exposed to several environmental stresses, all affecting plant growth and development, which consequently hampers the productivity of crop plants (Seki et al. 2003; Farooq et al. 2009a, b, 2011). Drought is considered the single most devastating environmental stress, which decreases crop productivity more than any other environmental stress (Lambers et al. 2008).

A continuous shortfall in precipitation (meteorological drought) coupled with higher evapotranspiration demand leads to agricultural drought (Mishra and Cherkauer 2010). Agricultural drought is the lack of ample moisture required for normal plant growth and development to complete the life cycle (Manivannan et al. 2008). Drought severely affects plant growth and development with substantial reductions in crop growth rate and biomass accumulation. The main consequences of drought in crop plants are reduced rate of cell division and expansion, leaf size, stem elongation and root proliferation, and disturbed stomatal oscillations, plant water and nutrient relations with diminished crop productivity, and water use efficiency (WUE) (Li et al. 2009; Farooq et al. 2009a). Climate models have predicted increased severity and frequency of drought under the ongoing global climate change scenarios (IPCC 2007; Walter et al. 2011).

Water deficit accelerates abscisic acid (ABA) biosynthesis, which decreases stomatal conductance to minimize transpirational losses (Yamaguchi-Shinozaki and Shinozaki 2006). To cope with such challenges, understanding the effects of drought on plants and morphological and physiological adaptations is crucial (Yamaguchi-Shinozaki and Shinozaki 2006). This chapter presents an overview of the effects of drought on morphology, water relations, nutrient uptake, and assimilation in crop plants; morphological and physiological mechanisms of drought resistance; and suggests some pragmatic options and strategies to cope with this global challenge.

1.2 Effects of Drought Stress

Deficit water supply at any growth stage poses detrimental effects on crop growth and development in general but varies depending on the severity of stress and the crop growth stage. Effects of drought on morphological, physiological, and biochemical processes in plants are discussed below.

1.2.1 Plant Growth and Productivity

Establishment of an early and optimum crop stand is important for harvesting maximum productivity. However, if the crop experiences an early drought, thereby affecting germination, then the suboptimal plant population is the major cause of low grain yield. Early season drought severely reduces germination and stand establishment principally due to reduced water uptake during the imbibition phase of germination, reduced energy supply, and impaired enzyme activities (Okcu et al. 2005; Taiz and Zeiger 2010).

Growth is an irreversible increase in volume, size, or weight, which includes the phases of cell division, cell elongation, and differentiation. Both cell division and cell enlargement are affected under drought owing to impaired enzyme activities, loss of turgor, and decreased energy supply (Kiani et al. 2007; Farooq et al. 2009a; Taiz and Zeiger 2010). For example, drought decreases growth and productivity of sunflower (*Heliantus annuus* L.) owing to reductions in leaf water potential, rate of cell division, and enlargement primarily due to loss of turgor (Kiani et al. 2007; Hussain et al. 2009). Under drought, reduced dry matter accumulation occurs in all plant organs, although different organs manifest varying degrees of reduction. For instance, drought decreased shoot and flower fresh and dry weights of marigold (*Tagetes erecta* L.) plants (Asrar and Elhindi 2011). Likewise, drought considerably reduced shoot and root dry weights in Asian red sage (*Salvia miltiorrhiza* L.), although roots were less affected than shoots (Liu et al. 2011). Drought also decreased leaf area owing to loss of turgor and reduced leaf numbers (Farooq et al. 2010a).

Leaf area index (LAI) is the ratio of leaf area to ground area, which denotes the extent of assimilatory power of crops under field conditions. Drought decreases LAI in crop plants in general. For instance, Hussain et al. (2009) reported decline in LAI of sunflower exposed to drought at budding and flowering stages. Drought also suppresses leaf expansion and tillering (Kramer and Boyer 1995), and reduces leaf area due to early senescence (Nooden 1988). All these factors contribute to reduced dry matter accumulation and grain yield under drought.

The study of different growth and developmental events in crop plants with respect to time is called crop phenology. Drought strongly affects crop phenology by shortening the crop growth cycle with a few exceptions. Limited water supply triggers a signal to cause an early switching of plant development from the vegetative to reproductive phase (Desclaux and Roumet 1996). For instance, total growth duration of both bread wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) decreased under drought (McMaster and Wilhelm 2003), which generally results in substantial yield reductions. The effect of drought is phase specific in most cases. For example, drought at pre-anthesis delayed flowering in quinoa (*Chenopodium quinoa* Wild.) and bread wheat plants (Majid et al. 2007; Geerts et al. 2008). Likewise, drought at anthesis commonly delays flowering in rice (*Oryza sativa* L.); interestingly, the longer the delay, the higher the yield penalty (Fukai 1999). In soybean (*Glycine max* L.), drought during grain filling hastened maturity but yield was down due to smaller grains (Desclaux and Roumet 1996).

Different crops respond to drought differently. For instance, upon exposure to drought flowering is delayed in maize (*Zea mays* L.) (Abrecht and Carberry 1993), quinoa (Geerts et al. 2008), and rice (Fukai 1999), whereas in soybean (Desclaux and Roumet 1996), wheat, and barley (McMaster and Wilhelm 2003) drought hastened flowering and physiological maturity.

While drought occurs during the vegetative period of crop growth, it may substantially decrease economic yield. Drought stress during reproductive and grain filling phases is more devastating (Table 1.1; Reddy et al. 2003; Vijay 2004; Yadav et al. 2004; Lafitte et al. 2007). Drought at flowering is critical as it can increase pollen sterility resulting in hampered grain set. In sunflower, for example, under drought at flowering, achene yield declined primarily due to less achenes (Hussain et al. 2008). In pearl millet (*Pennisetum glaucum* L. Leeke), drought at flowering increased the rate of ear abortion due to a decline in assimilate supply to developing ears (Yadav et al. 2004). In drought-stressed maize, kernel set was lost leading to low grain yield (Schussler and Westgate 1995). Likewise, water deficit at anthesis increased pod abortion which reduced yield in soybean (Liu et al. 2003).

1.2.2 Plant Water Relations

Relative water contents (RWC), leaf water potential, osmotic potential, pressure potential, and transpiration rate are the major attributes of plant water relations (Kirkham 2005), which are significantly affected under water deficit owing to

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