

Ricardo Aroca *Editor*

Plant Responses to Drought Stress

From Morphological
to Molecular Features

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Preface

Since plants are sessile organisms, they have to develop multiple strategies to cope with environmental constraints. One of the most common and damaging environmental stress is soil drought. The soil drought characteristics may vary from intervals of water scarcity and water depletion to prolonged periods of water deprivation or to long periods of soil water contents below the full capacity. Hence, the drought experienced by desert plants is not the same that for agricultural ones, or plants grown in Mediterranean climatic areas. So, each specific plant is adapted to their specific water soil conditions. At the same time, the responses of plants to drought varied from morphological ones to molecular, including physiological and biochemical ones too.

This book is intended to complete a comprehensive review about all aspects of the response of plants to drought. In each chapter a basic concepts will be first exposed, followed by the last findings of each topic. The first chapter is an overview of the effects and responses of plants to drought stress. The following chapters are subdivided in five parts: Morphological and anatomical responses, Physiological responses, Biochemical and Molecular responses, Ecophysiological responses, and Field responses. [Chapters 2 and 3](#) will deal about the morphological and anatomical adaptations of plants in response to drought. [Chapter 4](#) will deal with how water is up taken from the soil. [Chapters 5 and 6](#) will focus on how photosynthesis and water use efficiency is regulated under drought conditions. [Chapter 7](#) will deal about how drought stress affects nutrients uptake and assimilation. [Chapters 8–10](#) will tackle different biochemical drought responses such as osmotic adjustment, antioxidant systems or hormones. [Chapter 11](#) will deal with molecular aspects of the drought response. [Chapter 12](#) will tackle the particularities of tree response to drought. [Chapters 13–15](#) will review how different soil beneficial microorganisms change the response of plant to drought. Finally, [Chap. 16 and 17](#) will deal with the plant responses to drought under field conditions.

The potential readers of this book will be any graduate student or established researcher who wants to know basic concepts of plant responses to drought, as well as such researchers specialized in studies of plant response to drought stress.

Dr. Ricardo Aroca

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Chapter 1

Drought Stress in Plants: An Overview

M. Farooq, M. Hussain, Abdul Wahid and K. H. M. Siddique

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_2O_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^{\cdot}	Single oxygen
OH^-	Hydroxyl radicals
OsRDPCs	<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 (*Helianthus 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

Table 1.1 Decrease in grain yield in different crops by drought stress

Growth stage	Crop	Stress type	Yield reduction (%)	Reference
Reproductive	Rice	Mild stress	54	Lafitte et al. (2007)
Reproductive	Rice	Severe stress	94	Lafitte et al. (2007)
Reproductive	Rice	–	24–84	Venuprasad et al. (2007)
Flowering	Rice	Short severe stress	54	Lanceras et al. (2004)
Flowering and grain filling	Rice	Prolonged severe stress	84	Lanceras et al. (2004)
Flowering and grain filling	Rice	Prolonged mild stress	52	Lanceras et al. (2004)
Reproductive	Wheat	Prolonged mild stress	50–66	Kiliç and Yağbasanlar (2010)
Pre-anthesis	Wheat	Prolonged mild stress	18–53	Majid et al. (2007)
Post-anthesis	Wheat	Prolonged mild stress	13–38	Majid et al. (2007)
Terminal	Wheat	Prolonged mild stress	32–63	Majid et al. (2007)
Flowering and grain filling	Wheat	Prolonged mild stress	58–92	Dhanda and Sethi (2002)
Stem elongation	Wheat	Mild stress	18	Akram (2011)
Anthesis	Wheat	Mild stress	8	Akram (2011)
Stem elongation + anthesis	Wheat	Mild stress	22	Akram (2011)
Vegetative growth stage	Wheat	–	40	Allahmoradi et al. (2011)
Reproductive growth stage	Wheat	–	4	Allahmoradi et al. (2011)
Immediately prior anthesis	Sunflower	Mild stress	5–56	Chimenti et al. (2002)

decrease in water supply. Drought lowered RWC in tomato (*Solanum lycopersicum* L.) and caper bush (*Capparis spinosa* L.) (Subramanian et al. 2006; Ozkur et al. 2009). Water potential significantly declined in soybean roots, leaves, and pods under drought in general; however, root water potential dropped much earlier than leaves and pods (Liu et al. 2004). In sunflower, RWC, leaf water potential and osmotic potential were affected by drought (Tezara et al. 2002). However, different genotypes behaved differently; drought-tolerant genotypes maintained higher leaf water potential for longer and wilted later than sensitive genotypes upon exposure to drought (Ouvrard et al. 1996). Effects of drought also depend on the intensity and duration of drought. Tissue water contents decreased linearly with increased severity of drought (Reddy et al. 2004).

Transpiration not only helps to maintain leaf temperature but also drives water and nutrient uptake and CO₂ influx. Rise in leaf temperature of bread wheat and rice

plants is reported under drought owing to reduced transpiration rates (Siddique et al. 2001). de Campos et al. (2011) reported reduced turgor pressure and transpiration rate in citrumelo (*Citrus trifoliata* L.) rootstocks grown under drought.

Dry matter produced per unit of water consumed is termed WUE. WUE of genotypes and crops varies under drought. Abbate et al. (2004) and Subramanian et al. (2006) reported higher WUE in wheat and tomato under drought than well-watered controls mainly due to reduced transpiration rates under drought. However, in potato (*Solanum tuberosum* L.), early season drought substantially reduced WUE (Costa et al. 1997). Crop stage is also important in defining the effect of drought on WUE. For instance, drought stress decreased WUE in sunflower; however, the extent of the reduction was significantly higher when stress was imposed at flowering than at budding (Hussain et al. 2009).

1.2.3 Mineral Uptake and Assimilation

Nutrients used for plant growth and biomass production generally come from the internal cycling of reserve materials, which require water for their solubilization and translocation (Singh and Singh 2004). Limited nutrient uptake is a general phenomenon in crop plants grown under water deficit. Subramanian et al (2006) reported reduced nitrogen (N) and phosphorous (P) contents in roots and shoots of tomato seedlings grown under drought. Similarly, McWilliams (2003) reported reduced N and potassium (K) uptake in cotton (*Gossypium hirsutum* L.) under drought. In marigold seedlings, P content under drought was severely reduced (Asrar and Elhindi 2011).

Nutrient absorption is governed by interactions at the soil–root interface, including (1) root morphology and growth rate, (2) nutrient absorption kinetics of the roots; and (3) soil nutrient supply (Gutierrez-Boemand and Thomas 1999). Decreased soil water availability affects the rate of diffusion in many plant nutrients and finally the composition and concentration of soil solution (Singh and Singh 2004). With limited water supply, nutrient uptake by roots decreases because a decline in soil-water potential slows the diffusion rate of nutrients between the soil matrix and root surface (Farooq et al. 2009a). Lower transpiration rate and impaired active transport, due to a lack of energy input and altered membrane permeability, decreases root nutrient adsorbing power of crop plants under drought (Kramer and Boyer 1995; Baligar et al. 2001).

Impaired enzyme activity involved in nutrient assimilation under drought stress also disturbs nutrient acquisition. The activity of nitrate reductase in leaves and nodules of common bean (*Phaseolus vulgaris* L.) and dhainicha (*Sesbania aculeata* L.) is substantially decreased under drought (Ashraf and Iram 2005).

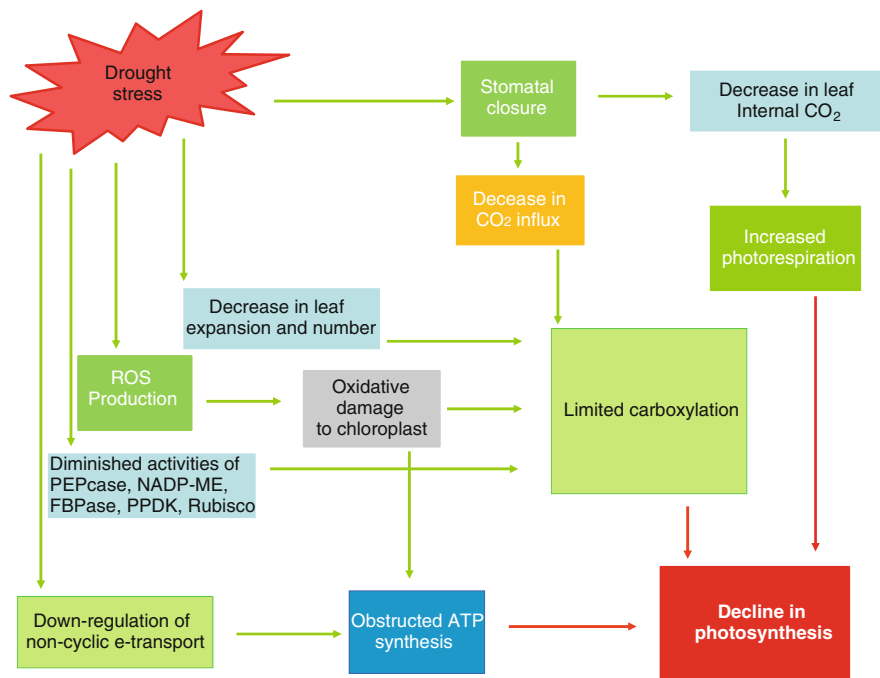


Fig. 1.1 Possible mechanism in which photosynthesis declines under drought. Drought disturbs the balance between production of ROS and antioxidant defense causing accumulation of ROS, which induces oxidative stress. With stomatal closure, CO₂ influx, and leaf internal CO₂ decrease which not only reduces carboxylation directly but also directs more electrons to form ROS and promotes photorespiration. Severe drought limits photosynthesis due to a decline in activities of ribulose-1, 5-bisphosphate carboxylase/oxygenase (*Rubisco*), phosphoenolpyruvate carboxylase (*PEPCase*), NADP-malic enzyme (*NADP-ME*), fructose-1, 6-bisphosphatase (*FBPase*), and pyruvate orthophosphate dikinase (*PPDK*). Drought limits photosynthetic area owing to reduced leaf expansion and leaf number. Moreover, non-cyclic electron transport is downregulated to match the reduced requirements of NADPH production and thus reduces ATP synthesis

1.2.4 Light Harvesting and Carbon Fixation

Efficient fixation of CO₂ by crop plants is vital for growth and productivity. Plants fix atmospheric CO₂ to organic compounds in photosynthesis. Photosynthesis is very sensitive to drought, as drought directly influences the photosynthetic capacity of crops. Reductions in leaf area (size and number) and stomatal closure, impaired activities of carboxylation enzymes and ATP synthesis, and destruction of photosynthetic apparatus are among the key factors lowering carbon fixation under drought (Fig. 1.1; Barlow 1988; Yamance et al. 2003). In general, effects of drought on carbon fixation can be divided into stomatal and non-stomatal limitations. Stomatal closure is one of the primary responses of crop plants upon exposure to drought. Stomatal closure helps reduce transpirational water loss with

a simultaneous decrease in stomatal CO₂ influx (Medrano et al. 2002; Flexas et al. 2004). Miyashita et al. (2005) reported decreased photosynthesis and transpiration rates due to reduced stomatal conductance in kidney beans (*Phaseolus vulgaris* L.). Likewise, drought stress progressively decreased CO₂ assimilation rates owing to reduced stomatal conductance in coconut (*Cocos nucifera* L.) plants (Gomes et al. 2010).

Reduced stomatal size is the dominant limitation to photosynthesis under mild to moderate drought stress. Reduced water potential and loss of turgor are responsible for reduced stomatal aperture; a decline in stomatal conductance due to diminished water and turgor potential is noted in sunflower under drought (Correia et al. 2006); nonetheless, stomata may also be closed without leaf dehydration. Carbon assimilation and stomatal conductance of intact sunflower leaves decreased with increasing degree of drought (Iqbal et al. 2009). Decreased stomatal aperture limits CO₂ influx resulting in a decline in the rate of photosynthesis. Although stomatal limitations may be the key factor responsible for the decline in rate of photosynthesis under some circumstances, non-stomatal limitations may be more important in other situations (Farooq et al. 2009a; Signarbieux and Feller 2011). Even avoiding stomatal limitations is not enough to overcome the detrimental effects of reduced stomatal conductance on photosynthesis under drought indicating the involvement of non-stomatal limitations (Tezara et al. 1999). Decreased synthesis and altered activities of essential enzymes and photosynthetic pigments, impaired ATP synthesis, photorespiration and heavy oxidative load are among the major non-stomatal limitations of carbon fixation (Farooq et al. 2009a).

Impaired activities of essential photosynthetic enzymes such as ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), phosphoenolpyruvate carboxylase, pyruvate phosphate dikinase, NADP-malate dehydrogenase, and NADP-malic enzyme are responsible for reduced rates of photosynthesis under drought (Reddy et al. 2004; Farooq et al. 2009a, b). Progressive downregulation and inhibition of metabolic processes leads to decreased ribulose-1,5-bisphosphate (RuBP) contents, which becomes the dominant limitation under severe drought, and thereby inhibits photosynthetic CO₂ assimilation (Flexas and Medrano 2002). The conversion of RuBP to 3-phosphoglyceric acid (3-PGA) decreases with decreasing leaf RWC suggesting that regeneration of RuBP is substantially inhibited under drought (Flexas and Medrano 2002). Therefore, declining RuBP contents and its regeneration are responsible for the rapid decline in photosynthesis under drought (Reddy et al. 2004). Based on maximum photosynthetic efficiency (A_{\max}) and carboxylation velocity of Rubisco ($V_{c,\max}$), Signarbieux and Feller (2011) reported strong non-stomatal limitations to photosynthesis in different grasslands species under drought at three different altitudes. Further, they highlighted that $V_{c,\max}$ is highly sensitive to water deficit and might represent a tool to evaluate the drought response of various species for grassland performance.

Photorespiration is also responsible for the decline in carbon fixation especially in C₃ plants under drought. As Rubisco is the key enzyme in CO₂ assimilation in C₃ plants and, due to its dual nature, it may act as carboxylase or oxygenase depending

upon leaf internal concentration of CO_2 or O_2 . Therefore, at moderate water stress, Rubisco acts as oxygenase due to higher internal O_2 than CO_2 contents owing to stomatal closure, and increase photorespiration at the expense of carbon-fixation (Ghannoum 2009). Under acute water deficit, photorespiration may be beneficial in three ways: (1) it is involved in energy dissipation and consequently reduces photoinhibition (Flexas and Medrano 2002), (2) it produces glycine (amino acid) that is used for glutathione synthesis, a component of antioxidant defense (Noctor et al. 1999), and (3) it enhances the RuBP supply to Calvin cycle (Wingler et al. 2000). In parallel to these benefits, photorespiration amplifies oxidative stress in photosynthetic tissues with elevated production of H_2O_2 in the peroxisome through glycolate oxidase; and more than 70 % H_2O_2 generation in C_3 plants under drought is related to photorespiration (Noctor et al. 2002).

The role of photosynthetic pigments such as chlorophyll (chl) contents, carotenoids, and xanthophylls are also vital in carbon fixation, as they are involved in capturing solar radiation to drive the photosynthetic mechanism. Drought stress severely decreased chl a and chl b contents in marigold (Asrar and Elhindi 2011). Similarly, water stress diminished the photosynthetic rate with declining photochemical efficiency (F_v/F_m) of chl fluorescence in primary leaves of kidney beans (Miyashita et al. 2005).

As mentioned earlier, low CO_2 influx under moderate and severe drought impaired RuBP contents, Rubisco activities or ATP synthesis which downregulates carbon fixation; consequently, oxidation of reduced nicotinamide adenine dinucleotide (NADPH) in the Calvin cycle is lowered. As a result, NADP^+ (primary electron acceptor) is not sufficiently available. Therefore, when drought-stressed plants are exposed to high irradiance, overproduction of ROS results in photoinhibition (Flexas and Medrano 2002). In canary pine (*Pinus canariensis* L.) exposed to moderate drought, for instance, rate of net photosynthesis was significantly reduced primarily owing to overproduction of ROS and reduced stomatal conductance (Tausz et al. 2001). Similarly, Pompelli et al. (2010) reported higher lipid peroxidation in jatropha (*Jatropha curcas* L.) plants due to decreased stomatal conductance under drought stress.

Plants exposed to almost all kinds of abiotic stresses including drought leads to elevated oxidative stress with overproduction of ROS, which are highly toxic and cause damage to proteins, lipids, carbohydrates, and DNA (Farooq et al. 2009a, b, 2011). Superoxide radicals (O_2^-), single oxygen (O_2^1), hydrogen peroxide (H_2O_2), alkoxy radicals (RO), and hydroxyl radicals (OH^-) are among the major ROS generated in plants under abiotic stresses (Apel and Hirt 2004). These ROS are highly reactive and deteriorate normal plant metabolism through oxidative damage to lipids, protein, and other macromolecules in the absence of any protective mechanism (Rout and Shaw 2001). In chloroplasts, PSI and PSII and in mitochondria, complex I, ubiquinone and complex III of electron transport chain (ETC.) are the major sites of generation of ROS (Gill and Tuteja 2010). Therefore, impaired activities of essential enzymes and ATP synthesis due to oxidative damage hamper photosynthetic and respiratory activities. Increased lipid peroxidation due to overproduction of ROS is reported in caper bush seedlings under

drought (Ozkur et al. 2009). Likewise, Qiu et al. (2008) reported higher lipid peroxidation (as indicated by MDA) in young wheat seedlings exposed to drought due to build up of O_2^- and H_2O_2 .

1.3 Drought Resistance Mechanisms

Plants undergo several morphological and biochemical adaptations at subcellular, cellular, and organ level to survive under drought. As far as crop production in a farmer's field is concerned, survival without a rational yield for subsistence requirement is not sufficient. Only a genotype producing higher grain yield compared with others under drought is truly drought resistant (Fukai and Cooper 1995; Kiliç and Yağbasanlar 2010). However, drought tolerance is a complex phenomenon associated with cuticle thickness, stomatal regulation, root system, hormonal balances, antioxidant defense system, osmotic adjustment, and maintenance of tissue water contents, etc. An overview of drought resistance mechanisms at various levels in crop plants is briefly described.

1.3.1 Morphological Adaptations

Drought escape, dehydration avoidance, and dehydration tolerance are important adaptive mechanisms of plants exposed to drought; a brief account of these adaptations is given below.

1.3.1.1 Drought Escape

Drought escape is the ability of a plant to complete its life cycle before the onset of drought and to undergo dormancy before the onset of the dry season. It is a general phenomenon in some desert plants, which exhibit extremely short life cycles and produce seeds during short rainy seasons in order to save them from extinction (Levitt 1980). Some extremely short duration crops and even genotypes within a species exhibit drought escape, but this always taxes yield (Turner et al. 2001). Drought escape is more advantageous where chances of terminal drought are more recurrent; as short-duration cultivars frequently escape terminal drought compared with late maturing cultivars (Meyre et al. 2001).

Matching crop phenology to prevailing growing conditions seems advantageous especially in terminal drought-prone areas. However, flowering may be critical as flowering time is a major trait of crop adaptation in areas where the growing season is restricted by terminal drought (Meyre et al. 2001).

1.3.1.2 Drought Avoidance and Phenotypic Flexibility

Drought avoidance is the ability of a plant to sustain high plant water status or cellular hydration under drought (Blum 2005). Plants accomplish this mechanism either by catching more water from the soil or by minimizing water loss through transpiration (Blum 2005).

Plants undergo certain morphological and physiological changes to minimize stress-induced losses; and considerable flexibility among crop species and even within species exists. Reduced biomass is a common phenomenon under drought; however, the extent of the reduction varies as different plant organs are affected differently. Drought reduced both shoot and root dry weight in Asian red sage (*Salvia miltiorrhiza* Bunge) but the effect was more severe on shoots, which enhanced the root-shoot dry weight ratio (Liu et al. 2011).

Crops plants more able to extract water from the entire soil profile can better resist drought. Root plasticity is the ability of a genotype to regulate its root growth pattern in accordance with prevailing constraints (Yamauchi et al. 1996). More rooting depth, root proliferation, and root length density commensurate with fetching more water are considered drought avoidance traits (Matsui and Singh 2003; Wang and Yamauchi 2006). A more prolific and deeper root system is imperative under drought as roots are the only organ capable of extracting water from the soil profile (Kavar et al. 2007; Gowda et al. 2011). Genotypes with more root growth in stress-prone environments are preferred. Drought stress inhibited root growth in general, even in tolerant genotypes, but the effect was more prominent on sensitive wheat genotypes due to an overall decrease in newly synthesized cell wall polysaccharides such as pectins, hemicelluloses, and cellulose (Piro et al. 2003). Likewise, peanut (*Arachis hypogaea* L.) genotypes with more root dry weight and root length density in deeper soil layers produced more pod yield than genotypes with less root dry weight and length exposed to water stress at pre-flowering (Jongrunklang et al. 2011).

Reduced leaf size is well correlated with drought stress; many xerophytes have small leaves as their adaptation to survive in harsh environments. As earlier mentioned, a small leaf area is advantageous to restricted water use and also responsible for low productivity of crops (Sinclair and Muchow 2001) but different crops or genotypes behave differently.

Reduced transpirational water loss is another important adaptation of drought avoidance. To attain that, plants have developed several morphological adaptations such as higher root–shoot ratios with fewer and smaller leaves to withstand water-deficit conditions by maintaining water budget with higher uptake and minimal loss (Lei et al. 2006). Increased stomatal and cuticular resistance, less small stomata, smaller leaf area, and vertical leaf orientation are among the major drought avoidance traits to minimize transpiration in order to save water under stress conditions (Sinclair and Muchow 2001; Wang and Yamauchi 2006). However, reduced leaf area and plant stature are advantageous for restricted water use but may also result in low productivity of crop plants (Sinclair and Muchow 2001).

1.3.2 Physiological Adaptations

Dehydration-tolerant plants maintain metabolic activities at low tissue water potential. Osmotic adjustment, antioxidant defense system, and changed dynamics of phytohormones are among the major physiological adaptations of plants under drought.

1.3.2.1 Osmotic Adjustment

Inadequate water availability in drought-prone environments affects the growth and productivity of crops by lowering tissue water status and turgor (Kiani et al. 2007; Hussain et al. 2009). Accumulation of organic and inorganic solutes under drought and/or salinity, which help lower water potential without decreasing actual water contents, is referred to as osmotic adjustment or osmoregulation (Serraj and Sinclair 2002). Nonetheless, these solutes do not pose any detrimental effects on membranes, enzymes, and other macromolecules, even at higher concentration, and are also called compatible solutes (Cechin et al. 2006; Kiani et al. 2007). These compatible solutes include soluble sugars, sugar alcohols, proline, glycinebetaine (GB), organic acids, trehalose, etc., (Cechin et al. 2006; Kiani et al. 2007; Farooq et al. 2008, 2009a, b). These compatible solutes not only help to maintain turgor pressure but also to protect the enzymes and macro molecules of cells from the damaging effects of ROS (Farooq et al. 2009a, b).

Osmotic adjustment is the key adaptation of plants at the cellular level to minimize the effects of drought-induced damage in crop plants (Blum 2005) and helps plants under drought in two ways: (1) it helps maintain leaf turgor to improve stomatal conductance for efficient intake of CO₂ (Kiani et al. 2007), and (2) it promotes the root's ability to uptake more water (Chimenti et al. 2006).

Under drought, greater accumulation of compatible solutes such as free proline, free amino acids, and GB may take place (Manivannan et al. 2007; Farooq et al. 2008). Proline is an important compatible solute which accumulates in plants exposed to dehydration stress, particularly in younger leaves (Perez-Perez et al. 2009). High levels of free proline allow the plant to maintain low water potentials (Jalil et al. 2007; Sankar et al. 2007) and derive water from the environment. It is not only involved in osmoregulation but also protects plants from osmotic stress (Sankar et al. 2007). Recently, de Campos et al. (2011) explored the role of elevated endogenous proline levels on gas exchange, antioxidant enzymatic activities, and water relations in leaves of transgenic citrangelo rootstocks equipped with *P5CSF129A* gene coding for the synthesis of key enzyme for proline synthesis under drought stress. Better turgor pressure highlighted the importance of osmotic adjustment with elevated endogenous proline accumulation. Higher turgor pressure in leaves of transgenic plants promoted stomatal conductance, photosynthetic rate, and transpiration rate compared with non-transgenic plants. They suggested that higher endogenous proline contents in transgenic plants are

not only involved in osmoregulation but also participate in leaf gas exchange and nullify the lethal effects of oxidative stress under drought conditions.

In addition to its function in osmoregulation (Wyn Jones et al. 1977), GB has been shown to protect functional proteins, enzymes (e.g. Rubisco), and lipids of the photosynthetic apparatus, and to maintain electron flow through thylakoid membranes (Xing and Rajashekar 1999). Therefore, osmotic adjustment by accumulating a variety of organic and inorganic solutes, along with higher activity of antioxidant enzymes in leaves, is among the imperative physiological adaptations of plants grown in drought-prone conditions (Lei et al. 2006).

1.3.2.2 Plant Growth Substances

Plant growth and development is regulated by certain growth substances produced internally called phytohormones or, if applied externally, plant growth regulators (PGRs). Phytohormones are needed in minute concentrations to modulate plant growth (Farooq et al. 2009a). Auxins, gibberellins (GA_3), cytokinins (Cks), ethylene, and ABA are the most studied phytohormones in higher plants. Of these, GA_3 and Cks promote plant growth (growth promoters), while ethylene and ABA have inhibitory effects (growth retardants) (Taiz and Zeiger 2010). Drought stress alters the endogenous synthesis of these growth substances. Generally, under stress conditions, the concentration of growth retardants increases at the expense of growth promoters to regulate plant water budget (Farooq et al. 2009a). For instance, drought altered the hormonal balance in common bean leaves, which included increased ABA content, a small decline in indole acetic acid (IAA) and GA_3 , and a sharp drop in zeatin content. Furthermore, a sharp decline in endogenous Cks contents amplified the response of shoots to increasing ABA content under drought (Figueiredo et al. 2008). The ABA and polyamine (PA) contents increased, while that of Cks decreased during a drought stress period in sunflower (Bano et al. 1994).

Under drought, Cks regulate plant responses via root-to-shoot signals (Rivero et al. 2007). Elevated ABA contents in plant organs under drought stress lead to many physiological changes to modulate plant growth. Higher ABA accumulation in roots under limited water supply signals the leaves to induce stomatal closure and avoid water loss via transpiration (Davies and Zhang 1991). ABA treatment on intact sunflower plants showed that K^+ -starved plants displayed faster water uptake, both in light and dark but the ABA treatment significantly inhibited water uptake during darkness over a 24 h cycle (Fournier et al. 2005).

Tomato seedlings treated with 1 μ M 24-epibrassinolide (EBR) nullified the negative effects of drought due to enhanced synthesis of endogenous ABA (Yuan et al. 2010). Salicylic acid (SA) is also a secondary metabolite accumulated in plants under drought stress, which is involved in inducing drought tolerance in plants by regulating several physiological processes through signaling. For instance, SA regulates drought-induced leaf senescence in perennials (Abreu and Munne-Bosch 2008). Leaf senescence in drought-stressed plants contributes to nutrient remobilization thus allowing the rest of the plant to benefit from the

nutrients accumulated during the lifespan of the leaf. Higher dry matter partitioning from stems and leaves to developing grains was noted in cultivars with more leaf senescence during grain filling under severe drought stress that ultimately helps to maintain grain yields (Kumar et al. 2006).

1.3.2.3 Antioxidant Defense System

Limited water supply under drought promotes oxidative stress with overproduction of ROS. Declined CO_2 influx with stomatal closure or impaired activities of enzymes and damaged photosynthetic apparatus under water stress downregulate photosynthesis leading to the generation of a variety of ROS such as O_2^- , O_2^{\cdot} , H_2O_2 , RO and OH^- (Flexas and Medrano 2002; Lawlor and Cornic 2002). These ROS are highly reactive and deteriorate normal plant metabolism through oxidative damage to lipids, protein, and other macromolecules in the absence of any protective mechanism (Rout and Shaw 2001). Plants douse the ROS through their antioxidant defense system with enzymatic and non-enzymatic components (Li 2008; Simova-Stoilova 2008; Hussain et al. 2008).

Of the enzymatic antioxidants, superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), glutathione reductase (GR), and ascorbate peroxidase (APX), and non-enzymatic antioxidants, ascorbic acid, α -tocopherol, reduced glutathione, β -carotene, PAs, salicylates, compatible solutes such as proline and GB and zeaxanthin accumulate in higher plants under drought stress to avoid oxidative damages (Scandalios 2005; Li 2008; Ozkur et al. 2009; 2010b).

Plants enhance the production of antioxidants in order to minimize detrimental effects of oxidative stress to normalize their metabolic activities under drought-induced oxidative stress (Fig. 1.2). It is generally accepted that O_2^- might be converted to H_2O_2 and then metabolized to water by APX and GR in plants to maintain membrane structures (Foyer and Fletcher 2001). Likewise, several other antioxidant enzyme molecules are responsible to counteract the deleterious effects of ROS. Initially, SOD catalyzes the conversion of O_2^- to H_2O_2 that is further reduced to water by APX by using ascorbate as an electron donor (Scandalios 2005). Elevated accumulation of antioxidant enzymes such as SOD, CAT, GR, APX, and POX are involved in lowering oxidative injury in caper bush seedlings under drought stress (Ozkur et al. 2009). Improved activities of CAT, APX, and SOD by brassinolides (BRs) application decreased H_2O_2 and MDA contents in drought-prone tomato seedlings (Yuan et al. 2010).

The ascorbate–glutathione cycle is a more efficient enzymatic way to breakdown H_2O_2 than CAT and POX as indicated in sorghum and sunflower (Cakmak et al. 1993). Drought decreased cytosolic activities of monodehydroascorbate reductase, and POX, and increased cytosolic dehydroascorbate reductase activity; however, chloroplastic activities of monodehydroascorbate reductase and dehydroascorbate reductase as well as cytosolic activities of CAT and SOD were not affected by drought in sorghum. Activities of the enzymes involved in the ascorbate–glutathione cycle were higher in the cytosolic fraction than the

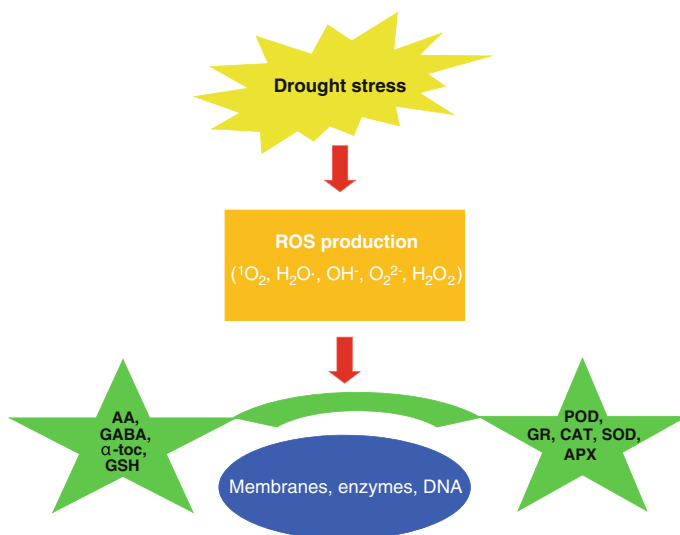


Fig. 1.2 Role of antioxidant enzymes in the ROS scavenging mechanism. Exposure to drought leads to generation of ROS, including singlet oxygen (1O_2), perhydroxyl radical ($H_2O\cdot$), hydroxyl radicals ($OH\cdot$), hydrogen peroxide (H_2O_2), and alkoxy radical (RO). The ROS attack membranes, enzymes and DNA, causing oxidative damage and impairing normal functions of cells. The antioxidant defense system in the plant cell includes both enzymatic and non-enzymatic constituents. Among the enzymatic components are peroxidase (POD), glutathione reductase (GR), catalase (CAT), superoxide dismutase (SOD), and ascorbate peroxidase (APX), whereas major constituents of the non-enzymatic antioxidant system are ascorbic acid (AA), γ -amino butyric acid (GABA), α -tocopherol (α -toc), and reduced glutathione (GSH). Upon exposure to drought, tolerant cells activate their antioxidant defense system, which then starts scavenging ROS and protecting the cell

chloroplasmic fraction in sorghum. But in sunflower, chloroplasts had higher enzymatic activities than cytosol. Because of differential localization of enzymes in cell fractions, it can be inferred that to detoxify H_2O_2 sorghum (C_4 plant) mainly uses the cytosolic ascorbate–glutathione cycle, whereas sunflower (C_3 plant) primarily uses the chloroplasmic ascorbate–glutathione cycle (Zhang and Kirkham 1996).

Higher free proline accumulation (1.5–2.1 times higher than control) in leaflets of coconut tree under drought stress decreased membrane damage (Gomes et al. 2008, 2010). Elevated accumulation of amino acids, proline, and GB accompanied by higher productivity in sunflower under drought stress highlights the protective role of these non-enzymatic antioxidants against oxidative damages under drought conditions (Manivannan et al. 2008; Hussain et al. 2008). Similarly, a decline in soluble sugar contents in rice anthers under drought stress impaired the ability to scavenge ROS and further intensify oxidative stress (Guan-fu et al. 2011).

1.3.3 Molecular Mechanism

Plants challenged with drought undergo many adaptive mechanisms at molecular levels to modulate water balance. Among them, up- and downregulation of many gene transcripts and accumulation of stress proteins is important (Kavar et al. 2007). A considerable rise in CDSP 32 (chloroplastic drought-induced stress protein) mRNA and protein was noted in potato under drought, which protected the chloroplast from drought-induced oxidative damage (Broin et al. 2000). Aquaporins are an important group of intrinsic membrane proteins able to assist passive exchange of water across membranes; these potentiate a 10- to 20-fold increase in water permeability by regulating hydraulic conductivity of membranes (Tyerman et al. 2002).

Many dehydration-responsive element-binding genes are also involved in signaling pathways in response to abiotic stresses including drought (Agarwal et al. 2006). The dehydration-responsive element/C-repeat (DRE/CRT) *cis*-acting element and its DNA-binding protein are a major transcription system modulating ABA-independent gene expression in response to drought and includes dehydration-responsive element binding proteins (DREB)/C-repeat binding factors (CBF) family of proteins. DREB2 subclass of DREB/CBF family proteins are expressed under drought to articulate genes involved in stress tolerance (Seki et al. 2003).

Signal transduction pathways are also induced in plants under drought to regulate growth. An early-warning response mechanism exists in plant roots to activate the hydrogen pump ATPase protein (H^+ -ATPase) on plasma membrane of root hairs before a substantial decline in plant RWC. The activation of root hair cell plasma membrane H^+ -ATPase triggers amplified biosynthesis of key osmolytes such as leaf proline and GB to maintain the water budget of plants. Moreover, interspecific and intraspecific differences in the timing of triggering early responses may exist and drought-tolerant cultivars to initiate warning responses much earlier than sensitive cultivars (Gong et al. 2010). PAs have been associated with the response of plants to drought via signaling, in addition to their roles in responses to many other stresses (Bae et al. 2008). Ornithine decarboxylase (TcODC), arginine decarboxylase (TcADC), S-adenosylmethionine decarboxylase (TcSAMDC), spermidine synthase (TcSPDS), and spermine synthase (TcSPMS) are the expression patterns of genes encoding enzymes involved in PA in cacao (*Theobroma cacao* L.) leaves. Expression of TcODC, TcADC, and TcSAMDC is induced at the start of drought which modulates stomatal conductance, photosynthesis, photosystem II efficiency, and leaf water potential. Induction of TcSAMDC in leaves is most closely correlated with changes in water potential. The earliest measured responses to drought, detected in cacao leaves 13 days after the onset of drought, were enhanced expression of TcADC and TcSAMDC in roots along with decreases in stomatal conductance, photosynthesis, and PS II efficiency due to elevated levels of putrescine, spermidine, and spermine (Bae et al. 2008).

1.4 Management of Drought Stress

Water-wise cultivation augmented with drought-tolerant crops and genotypes is the only option to feed the escalating world population. Development of crop genotypes requiring less water to produce unit biomass along with an accurate site-specific package of production technology is urgently needed to sustain crop productivity in drought-prone areas. Advancements in the field of genomics and biotechnology along with traditional breeding approaches seem viable to introduce transgenic plants to perform better under stress conditions. Nonetheless, exogenous application of certain osmoprotectants, growth regulators, and minerals are helpful to induce drought tolerance in otherwise susceptible plants.

1.4.1 Selection and Breeding Approaches

Mass screening and breeding approach is often used to explore genetic variability for drought tolerance among crop genotypes for desired agronomic traits to then breed genotypes better able to perform in drought-prone areas (Ashraf 2010). Several strategies such as induction of earliness for drought escape, modification in morphology that leads toward drought resistance, and introduction of drought-tolerant traits associated with high yield can be targeted in breeding programs to induce drought tolerance (Rauf 2008).

In most regions of arable cropping, droughts are unpredictable but do not generally occur every year. Selection and breeding efforts should therefore be targeted to develop genotypes producing good yield under both drought and well-watered conditions. Conventional breeding efforts focus on direct selection for yield under target environments (Atlin and Lafitte 2002). Since yield is a quantitative trait with low heritability and high genotype \times environment interactions (Babu et al. 2003), this approach is no more an attractive option (Farooq et al. 2009a). Mass screening of genotypes may therefore be done under managed or natural environments for certain stable secondary traits with highly heritable, easy to measure genetic associations with grain yield under drought but no association with yield reduction under optimal environments (Edmeades et al. 2001). However, some studies have reported the effectiveness of direct selection for grain yield under drought (Venuprasad et al. 2007; Kumar et al. 2008).

Developing short-duration genotypes often seems useful to avoid yield losses from late-season drought, as short life cycles help to avoid periods of stress (Kumar and Abbo 2001). However, these short-duration cultivars do not do well in a prolonged growing season. Therefore, genotypes with developmental plasticity are better under drought stress conditions, as they can to some extent adjust their life cycle according to the prevailing conditions (Levitt 1980).

Root characteristics, drought susceptibility index, and relative yield are among the important secondary traits, which may be used to select drought-tolerant

genotypes (Chimenti et al. 2002; Blum 2005; Kiani et al. 2007). According to Biao-lin et al. (2011), root length and number, root fresh weight, and relative water contents significantly influence drought resistance, which could thus be used as a comprehensive index for drought resistance at the seedling stage. Gowda et al. (2011) also opined to select genotypes with deep roots for improving drought resistance. Signarbieux and Feller (2011) reported that carboxylation velocity of Rubisco provides a rapid tool for screening genotypes for drought tolerance. Manivannan et al. (2008) reported osmotic adjustment as an important adaptive trait nullifying the bad effects of drought stress in sunflower.

1.4.2 Marker-Assisted Selection

Advancements in the field of biology and proteomics make it possible to identify various quantitative trait loci (QTL) and proteins associated with drought tolerance in crop plants; and these drought-related QTL and proteins can be used as markers in breeding programs to tailor drought-tolerant genotypes (Salekdeh et al. 2002; Lanceras et al. 2004; Farooq et al. 2009a, b; Ashraf 2010). After mapping QTLs for grain yield and related traits with simple sequence repeat/expressed sequence tag marker map, Kirigwi et al. (2007) explained substantial variation in chromosome 4A of wheat. A QTL located on rice chromosome 1 near *sd1* contributes 4–32 % of total genetic variation for grain yield under drought and optimal conditions, respectively, suggesting that this QTL is more responsible for varied grain yield of rice under stressful environments than under normal situations (Kumar et al. 2007).

Ke et al. (2009) identified 10 drought-responsive phosphoproteins in rice using proteomics approach. Similarly, Salekdeh et al. (2002) identified 16 drought-responsive proteins in rice; and among them, actin depolymerizing factor, S-like RNase homolog, and RuBP activase were upregulated and isoflavone reductase-like protein was downregulated under drought stress. LEA proteins accumulate in various crop plants exposed to drought-stressed environments (Babu et al. 2004; Gosal et al. 2009), acting as molecular chaperones and protecting the biological membrane from the damaging effects of dehydration stress (Browne et al. 2002; Babu et al. 2004). Substantial increases in chloroplastic drought-induced stress protein (CDSP 32) mRNA and protein was reported in potato under drought, which may preserve chloroplastic structures against oxidative injury upon drought (Broin et al. 2000).

Recently, Bae et al. (2011) identified five putative proteins in the rice genome database (<http://signal.salk.edu/cgi-bin/RiceGE>) named as *Oryza sativa* RING domain-containing proteins (OsRDCPs) possessing a single RING motif in their N-terminal regions. Of five identified proteins, OsRDCP1 is involved in physiological responses to neutralize the effects of drought stress. Nonetheless, OsRDCP1-overexpressing transgenic rice lines exhibited superior growth and dehydration tolerance than wild and OsRDCP1-mutant lines under water deficit.

Therefore, OsRDCP-1 can be used as a target protein for developing drought-tolerant rice genotypes in future. Proton-ATPase (H^+ -ATPase) is also an important protein located on the plasma membrane of root hair cells mediating root-to-shoot signaling under limited water supply and is actively involved in osmoregulation, maintaining water contents and other water stress-related mechanisms (Liu et al. 2005, 2008). Likewise, PebC1 a novel protein elicitor isolated and purified from *Botrytis cinerea* strain BC-4-2-2-1 (mold fungus) notably improved wheat seedling growth and the drought resistance integrated index from 36.53 to 57.08 under two cycles of drought stress. Nevertheless, phenylalanine ammonia-lyase (PAL), POD and polyphenol oxidase (PPO)-related resistance mechanisms also perked up after PebC1 treatment (Zhang et al. 2010).

Molecular and genetic approaches are also used to explore signal transduction pathways induced in plants in response to drought. Hydraulic properties of roots are regulated by root-sourced signals such as ABA (Mahdieh and Mostajeran 2009). DRE/CRT cis-acting element and its DNA-binding protein is a major transcription system including a DREB/CBF family protein that modulates ABA-independent gene expression under drought. DREB1/CBF and DREB2 are two subclasses of DREB/CBF family proteins generated under cold and drought stress, respectively, to articulate various genes involved in stress tolerance (Seki et al. 2003). Therefore, combined knowledge of traditional breeding along with marker-assisted selection makes it easier and more efficient to induce drought tolerance in crop plants.

1.4.3 Biotechnology and Functional Genomics

Advancements in biotechnology made it possible to identify drought-responsive genes to tailor plants with superior drought tolerance using the transgenic approach (Hadiarto and Tran 2011). Transfer of one or more genes from one species to another to induce some desired qualitative and quantitative traits is called the transgenic approach and plants are called transgenic plants. Compared with conventional breeding, the transgenic approach ensures induction of only desired genes and confines the entry of unwanted genes into an organism from the donor organism (Gosal et al. 2009). Cloning of stress tolerance-related genes and identifying their functions are crucial to augment crop tolerance to abiotic stresses including drought (Ashraf 2010). Plants with C_4 pathways exhibit higher photosynthesis rates, water use efficiency and higher biomass production, especially at low internal leaf CO_2 concentration, high temperature and drought stress. Efforts are underway to introduce this feature to C_3 plants by overproducing PEP carboxylase to improve photosynthetic efficiency and yield potential under drought (Bao-Yuan et al. 2011). Transgenic rice plants producing PEP carboxylase resist drought stress with a slow decline in photosynthetic rate. It is supposed that overproduction of PEP carboxylase might be involved in drought resistance to decrease the effect of drought stress on photosynthesis in rice (Bao-Yuan et al. 2011).

Elevated accumulation of compatible solutes such as proline and GB play a pivotal role in enhancing drought tolerance among a variety of crops with superior osmotic adjustment (Ashraf and Foolad 2007) and transferring genes to increase the endogenous accumulation of such solutes can improve drought tolerance of transgenic plants (Table 1.2). Recently, de Campos et al. (2011) studied the performance of transgenic ‘Swingle’ citrumelo rootstocks equipped with *P5CSF129A* gene to code the key enzyme for proline synthesis. Maintenance of turgor pressure in leaves of transgenic plants led to higher stomatal conductance, photosynthetic, and transpiration rates when compared to non-transgenic plants. Results suggest that transgenic plants coped better with water deficit than non-transgenic controls, as high endogenous proline levels acted not only by mediating osmotic adjustment, but also by contributing to gas exchange parameters and ameliorating deleterious effects of drought-induced oxidative stress by overproduction of APX and SOD.

Similarly, encoding genes to perk up endogenous accumulation of polyamines might help to alleviate damaging effects of water stress. *Arabidopsis thaliana* transgenic lines overexpressing arginine decarboxylase 2 gene (*ADC2*) contain high levels of Put without disturbing spermidine and spermine levels, even under drought stress, suggesting the role of Put in dehydration resistance. A notable reduction in transpiration rate with elevated stomatal closure is observed in the *ADC2* over-expresser lines compared with wild type, while the number of stomata remained unchanged. These findings confirm that the role of Put in drought induction in transgenic plants is related to avoiding the water loss via transpiration by regulating stomatal opening (Alcázar et al. 2010). However, this may tax crop yield since most probably photosynthesis was decreased.

1.4.4 Exogenous Application of Hormones and Osmoprotectants

Exogenous application of various PGRs and osmoprotectants can also enhance drought tolerance of crop plants. Foliar application of plant hormones and osmoprotectants such as GA₃, Cks, ABA, proline, GB, brassinolids, PAs, and SA has proven worthwhile to ameliorate stress effects with elevated osmotic adjustment to maintain turgor and antioxidants accumulation to detoxify ROS to maintain stability of membrane structures, enzymes, and other macromolecules under drought stress (Manivannan et al. 2008; Farooq et al. 2009c, d; Yuan et al. 2010; Alcázar et al. 2010; Anjum et al. 2011).

SA is a secondary metabolite that induces drought tolerance in plants by regulating several physiological processes through signaling. It plays an important role in producing tolerance against drought (Senaratna et al. 2000; Singh and Usha 2003). Exogenous application of methyl salicylic acid on leaves of water-stressed perennial plants promotes leaf senescence; as programmed leaf senescence in drought-stressed plants contributes to nutrient remobilization thus allowing the rest of the plant to benefit from the nutrients accumulated during the life span of the leaf (Abreu and Munne-Bosch 2008). Likewise, exogenous application of SA