Chapter 1
Understanding How Plants Respond to Drought Stress at the Molecular and Whole Plant Levels

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Abbreviations

A	Photosynthetic rate
ABA	Abscisic acid
ABFs	ABRE- binding factors
ABRE	ABA-responsive element
ACC	1-aminocyclopropane-1-carboxylic acid
AP2	APETALA 2
APX	Ascorbate peroxidase
AREB	ABRE-binding protein
AsA	Reduced ascorbate
ASH	Ascorbic acid
bZIP	Two basic leucine zipper transcription factors
CAT	Catalase
CBF	CRT binding factor
CRT	C-repeat
DA	Drought avoidance
DAG-PP	Diacylglycerol-pyrophosphate
DE	Drought escape
Dehydrin	Dehydration-induced
DHAR	Dehydroascorbate reductase
DRE	Dehydration-responsive element
DREB	DRE-binding protein
DT	Drought tolerance
E	Transpiration rate
ERF	Ethylene-responsive element binding factor
ETC	Electron transport chain
EUW	Effective use of water
GOPX	Guaicol peroxidase

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GPX	Glutathione peroxidase
GR	Glutathione reductase
GSH	Glutathione
GST	Glutathione-S- transferase
H_2O_2	Hydrogen peroxide
HI	Harvest index
LEA	Late embryogenesis proteins
LOX1	Lipoxygenase 1
LWP	Leaf water potential
MAPK	Mitogen-activated protein kinase
MDA	Malondialdehyde
MDAR	Monodehydroascorbate reductase
MDHAR	Monodehydroascorbate reductase
NAC	NAM, ATAF, CUC
NACR	NAC recognition sequence
NO	Nitric oxide
$O_2^{\cdot -}$	Superoxide anion
$^1O_2$	Singlet oxygen
OA	Osmotic adjustment
$^{\cdot}OH$	Hydroxyl radicals
P5CS	Delta (1)-pyrroline-5-carboxylate synthetase
PA	Phosphatidic acid
PCK	Phosphoenolpyruvate carboxylase
PEG	Polyethylene glycol
PLD	Phospholipase D
POD	Peroxidase
PP2C	2C-type protein phosphatase
PPDK	Pyruvate orthophosphate dikinase
PSI	Photosystem I
PSII	Photosystem II
PYL	Pyrabactin-resistance like
PYR	Pyrabactin resistance
QTL	Quantitative trait locus
RAB	Response to ABA
RCAB	Regulatory component of ABA receptor
ROS	Reactive oxygen species
Rubisco	Ribulose 1,5 bisphosphate carboxylase/oxygenase
RuBP	Ribulose 1,5 bisphosphate
SnRK2	Sucrose non-fermenting 1-related protein kinase
SOD	Superoxide dismutase
WUE	Water use efficiency

1.1 Introduction

With climate change and abnormal weather events, more frequent drought and other stresses such as heat and salinity are likely to occur all over the world [169, 185, 229]. Drought stress reduces plant growth and crop production [40, 90].

Drought stress induces a range of morphological, physiological, biochemical, and molecular changes in plants [178]. Plant growth (leaf expansion and size, leaf area index, plant height, plant branching, and plant tiller numbers) has been reduced when drought stress was imposed on plants during vegetative growth stages [92]. Under severe drought stress, plants senesce their leaves to reduce transpiration rate and water consumption [8, 165]. Drought has been reported to enhance plant growth and development, shorten the duration of the seed filling period, and remobilize the reserves in plant parts to growing seeds, resulting in a great reduction in the duration of the photosynthetic capacity of plants and lowering seed yield [34, 77, 198].

At the physiological and biochemical level, drought stress induces stomatal closure and consequently decreases photosynthetic rate, stomatal conductance, and transpiration rate [54, 121, 154]. Drought also inhibits the biochemistry of photosynthesis [141, 214]. Soluble solutes accumulate in plants under drought stress to maintain plant turgor pressure at a lower leaf water potential (LWP) in a process known as an osmotic adjustment (OA) [56, 208]. Production of reactive oxygen species (ROS) under drought stress can cause oxidative damages to lipids, cell nucleic acid, and proteins [22, 106]. Plants respond to the increase in ROS by producing nonenzymatic antioxidants or enzymatic defense (detoxification and scavenging enzymes) to prevent or reduce the oxidative damages of the ROS under drought stress [10, 106, 122, 132, 161, 240]. Protein synthesis is also changed in response to drought. Dehydrin proteins (Class II of LEA proteins) are induced in response to drought stress and have been shown to function in drought tolerance (DT) [38, 94, 123].

Plants also respond to drought at the molecular level. Drought stress induces the accumulation of ABA [131]. Drought stress and ABA induce drought-responsive and ABA-responsive genes mediated through ABA-independent and ABA-dependent regulatory pathways [23, 41, 211]. Other important signaling transduction pathways mediate drought-related gene expression such as strigolactone hormone [118], ROS [15, 113], lipid derived signaling [113, 167], soluble sugars, and others [55, 99]. Transcription factors such as ABREB/ABF, DREB1/CBF, DREB2, and NAC play an important role in the regulatory network of drought-related genes [169]. The drought-inducible genes include genes encoding important functional and regulatory proteins [189, 211, 212]. Genetically engineering plants to express the drought-inducible genes has shown drought stress tolerance and can be a promising tool to improve DT in plants [138, 229, 238].

Development of crops for enhanced drought resistance requires knowledge of morphological and physiological responses and genetic control of the contributing traits at different plant developmental stages [92]. This chapter summarizes whole plant growth and yield performance under drought to understand plant DT at the physiological and molecular levels. Understanding plant responses to drought at the morphological, physiological, and molecular levels and how these changes ameliorate the effect of drought stress on plant productivity is needed to improve plant stress tolerance using biotechnology, while maintaining the yield and quality of crop [28, 178]. Using a genetic engineering approach to produce transgenic plants by transferring a specific drought-related gene can improve DT in plants.

1.2 Drought Resistance and Adaptation Mechanisms

Drought resistance is a broad term applied to both wild species and crop plants with adapted traits that enable them to cope with water shortage [19]. Drought resistance mechanisms in plants have been classified into: (1) drought escape (DE) (the ability of plants to complete their life cycle in the presence of water before the onset of drought stress); (2) drought avoidance (DA) (the ability of plants to maintain tissue hydrated; DT at high water potential); (3) DT (the ability of plants to function while dehydrated; DT at low water potential; desiccation tolerance) [90, 220]. Plants that escape drought, such as desert ephemerals, annual crops, and pasture plants, exhibit earlier flowering, shorter plant life cycle, and developmental plasticity [20, 210]. *Brassica rapa* plants escape drought through early flowering rather than avoid drought through increased water-use efficiency [100]. *B. rapa* plants grown from seeds collected from natural populations after five consecutive years of drought had an evolutionary shift to a DE mechanism in which plants had an earlier flowering [100]. This mechanism of DE was related to lower water-use efficiency (high transpiration and inefficient water use), leading to rapid development and shortened growing season [100]. With respect to the DA mechanism, plants have two important strategies: enhancing water uptake from soil (roots traits); and reducing water loss from plants (stomatal characteristics and morph-anatomical traits such as leaf rolling, dense leaf pubescence, thick cuticle and epicuticular wax layer, heavily lignified tissue, smaller mesophyll cell and less intercellular spaces, reduced plant growth, and leaf senescence) [20]. Root growth rate, root volume, root depth, and root dry weight are traits related to DA [237]. In the third mechanism of plant resistance to drought (DT), plants can tolerate drought through OA, antioxidant defense mechanisms, dehydrins and late embryogenesis abundant (LEA) proteins, ABA response, desiccation tolerance [237], and water-use efficiency [measured as photosynthetic carbon gain (A) over transpiration water loss (stomatal conductance, g)] [20, 100]. Two water use strategies may be employed by woody plants: prodigal water use behavior (beneficial in a short interruption of water supply), and conservative water use behavior (beneficial in a long-term drought) [20]. In the first strategy (prodigal water use), plants had a high stomatal conductance, high carbon exchange rate, low water use efficiency, and plants grow faster [20]. In the second strategy (conservative water use), plants have higher water use efficiency, high capacity for drought resistance, and slow growth rate [20]. Thus higher drought resistance is sometimes linked to even or lower water use efficiency; however, in other cases, higher drought resistance is associated with high water use efficiency, indicating that drought resistance and water use efficiency are not synonymous terms [20]. It is impossible to assess the relative contributions of DE, DA, and DT to overall drought resistance at the whole-plant level in rice [237]. DT and DA traits had a distinct genetic basis [237]. The genetic variation in DE and avoidance in natural herbaceous populations is complex and controlled by many quantitative trait loci (QTL) of small effect, and gene × environment interactions, indicating genetic constraints limit the concurrent evolution of both DE and avoidance strategies [136].

In arid and semiarid regions where rainfall occurs during winter and spring and no rainfall during summer (dry condition), plants use different drought resistant mechanisms to cope with drought stress in these regions. In the DE mechanism, rapid phenological development of plants ensures that flowering and grain filling occur before the onset of water shortage and high temperature, which prematurely terminate the plant life cycle and reduce yield. Improved reproductive success by DE also includes better partitioning of assimilates and stored reserves from stem and root to developing fruits and seeds [20]. The acceleration of maturity (phenological adjustment), coupled with a high seed filling rate (shoot biomass distribution), reduced the negative effect of drought stress in the drought-resistant common bean cultivars (*Phaseolus vulgaris* L.) [196]. Despite the advantage of DE during the water shortage seasons, DE limits yield in years with plentiful rainfall. Other drought resistant mechanisms in arid and semiarid regions including an early vigor, a greater number of fertile flowers, a longer duration of seed growth, an increased harvest index (HI), an OA, a high assimilate transfer to the seed, a rapid grain growth, and high water-use efficiency have been shown to improve cereal yield in these water-limited regions [16, 19]. The ability of plants to save water and retain some residual soil moisture to the end of the season may also contribute to better yield [19]. In a Mediterranean legume crop such as lupine (*Lupinus luteus* L.), contrasting adaptive strategies to terminal drought-stress have been reported. Long-season, high-rainfall habitats select for traits (competitive traits) that are related to delayed phenology, high biomass, and productivity, leading to high water use and early stress onset, whereas terminal drought-prone environments select for the opposite traits (ruderal traits) that facilitate DE/avoidance but limit reproductive potential [30].

In subhumid regions where rainfall occurs during summer, the ability of summer crops to develop a rapid growth and flowering over an extended period (indeterminate growth habit) may reduce their vulnerability to drought stress compared with crops that set their flowering at a specific period (determinate growth habit). Indeterminate cultivars of soybean were better able to recover from water stress imposed preflowering and during early pod development and had greater seed yield after recovery from stress treatment than were determinate ones [228]. This increase in the yield of the indeterminate cultivars was associated with more pods per node rather than with other yield components, or with leaf area index or leaf area duration differences [228]. The indeterminate cultivars of cotton (*Gossypium hirsutum* L.)

had higher lint yields and irrigation water-use efficiency than did the determinate cultivars at the intermediate moisture level, suggesting that cotton cultivars with relatively indeterminate growth habit are better adapted to environments with limited soil moisture than cotton cultivars with relatively determinate growth habit [188].

1.2.1 Morphological Adaptation

An early response to drought stress is a reduction in plant growth. Plant growth is an irreversible process including cell division, cell elongation, and differentiation. Leaf elongation occurs as a balance among cell turgor pressure, cell wall threshold, and cell wall extensibility [220]. Under drought stress, cell turgor is less than cell wall threshold, which results in a reduction in leaf elongation and size and a retardation of plant growth [220]. Drought stress reduces leaf size, stem extension, and root proliferation [92]. Impaired enzyme activities, loss of turgor, and decreased energy supply under drought stress results in a reduction in both cell division and elongation [93, 220]. Loss of turgor under drought decreased growth and productivity of sunflower (*Heliantus annuus* L.) due to reductions in LWP, rate of cell division, and elongation [129]. Drought significantly reduced shoot and root dry weights in Asian red sage (*Salvia miltiorrhiza* L.), but the shoots were more affected than roots [147]. Although severe drought stress terminated root growth earlier and significantly decreased the rate of root growth as a result of inhibition of both cell elongation and cell production in a Sonoran desert cactus (*Pachycereus pringlei*, Cactaceae), the total number of lateral roots and primordia was the same under severe and well-watered conditions [81]. These results indicated that lateral root formation is a stable developmental process resistant to severe water stress and that water stress accelerates the determinate developmental program of the primary root, which are two important features for successful seedling establishment in a desert [81].

Another plant response to drought stress is leaf senescence and abscission [8] which is also an important factor in determining seed yield. Leaf senescence, mediated by enhancing the synthesis of endogenous plant hormone ethylene under drought stress [9, 12], determines the duration of photosynthesis and the seed filling period [13]. When drought stress occurred during late reproductive growth, leaf senescence was accelerated [67, 165]. Although leaf senescence under drought can be an adaptive mechanism to drought by reducing plant water consumption, leaf senescence reduces plant yield under drought.

Pandey et al. [182] reported that the increase in drought intensity decreased growth parameters such as leaf area index, leaf area duration, crop growth rate, and shoot dry matter of grain legumes. The reduction in leaf area under drought was due to the loss of turgor and reduced leaf number [91]. Seed yield of grain legumes was positively correlated with leaf area index, leaf area duration, crop growth rate, and shoot dry matter [182]. Black bean (*Phaseolus vulgaris* L.) exposed to water stress during vegetative growth had lower plant height and leaf area index than did well-watered plants [173]. Dry conditions resulted in 68 % reduction in leaf area index of soybean plants compared to irrigated conditions [70]. Drought decreased leaf expansion, tiller formation, and leaf area due to early senescence [129, 137, 175]. This reduction in leaf expansion and growth can be a way to adapt to drought by reducing plant water consumption (plant survival), but the reduction in plant growth under drought is related to the reduction in seed yield.

Drought stress has been reported to reduce seed yield and yield components and the intensity of this reduction depends on the growth stage at which drought occurs, showing that plants are most susceptible to water stress at the reproductive growth stage [198]. Drought stress imposed on soybean during vegetative growth decreased internode length and plant height [76]. When drought occurred during vegetative stages of rice, drought had only a small effect on subsequent plant development and grain yield, resulting in up to 30 % reduction in yield due to reduced panicle number per unit area or reduced number of spikelets per panicle [34]. Drought stress early during the reproductive stage can delay or inhibit flowering. In most studied species, the most stress-sensitive reproductive stage is the stage of meiosis [198]. In the mitotic stage of flowering, drought causes pollen sterility and only affects female fertility when stress is severe [14, 198]. When drought stress was imposed during the reproductive growth stage of wheat, pollen fertility was most affected [187]. The most sensitive stage of wheat yield to drought stress is in the early spikelet development (5 d after jointing) [187]. The rice and maize plants are highly susceptible to drought during flowering (anthesis) and early grain initiation, causing pollen sterility, failure of pollination, spikelet death, and zygotic abortion due to changes in carbohydrate availability and metabolism [172, 198]. Drought stress conditions modify source-sink relations by inducing premature senescence in the photosynthetic source tissues of the plant, by reducing the number and growth of the harvestable sink organs, and by affecting the transport and use of assimilates, thereby influencing plant growth, adaptive responses, and consequently crop yield [12, 13]. Drought stress strongly reduced the cell wall invertases (cwInv) activities, key metabolic enzymes regulating sink activity through the hydrolytic cleavage of sucrose into hexose monomers [12]. The most sensitive stage to drought in rice was observed when stress occurred during panicle development [34, 187], resulting in delayed anthesis, reduced number of spikelets per panicle, decreased percentage of filled grains, and consequently reducing grain yield to less than 20 % of the control (irrigated plants) [34]. Drought stress during pod lengthening (R_3–R_5) of soybean decreased the number of pods per vegetative dry matter unit [76]. Drought stress during grain development and filling shortened the grain filling period (prematurely terminated) and reduced seed size and weight [198]. Drought stress during early seed-fill of soybean [*Glycine max* (L.) Merr.] reduced the number of seeds per pod, whereas late stress during the seed filling period (after the abortion limit stage) decreased seed weight [76]. Drought stress during grain filling of rice hastened the plant maturity and reduced the percentage of filled grain and individual grain weight [34]. Genetic control of yield under reproductive-stage drought stress in rice showed that a QTL (*qtl12.1*) had a large effect on grain yield under stress, increased HI, biomass yield, and plant height while reducing the number of days to flowering [31]. In barley, drought stress during the grain filling period enhanced the grain growth rate, shortened the grain filling duration, decreased grain yield by reducing the number of tillers, spikes, and grains per plant, and individual grain weight, indicating that postanthesis drought stress was detrimental to grain yield regardless of the stress severity [201, 202, 205]. Late-terminal drought stress (rainfed) shortened reproductive growth duration and fastened maturity of chickpea plants, resulting in a decrease in seed yield by 49–54 % compared with irrigated plants, indicating that drought during the reproductive growth stage was detrimental to all genotypes studied (desi and kabuli) [206]. Other researchers have shown that desi chickpea genotypes (smaller, dark seeds) were generally more drought and heat tolerant than kabuli chickpea genotypes (larger, pale seeds) [44]. In muskmelon (*Cucumis melo* var. *reticulatus*) plants grown under three irrigation levels [0.5, 0.75, 1.0 actual evapotranspiration (AET)], decreasing the irrigation level decreased the length, diameter, weight, Brix, flesh firmness, seeds, and fertile seeds of melon fruit [11]. The best irrigation level for getting the highest total fruit yield was at 0.75 AET [11]. Drought stress during reproductive stages reduces photosynthetic rate, assimilates partitioning to expanding cells, which increases flower and pod abortion and decreases vegetative growth, duration of the seed filling stage, seed number, seed size, and consequently decreases total seed yield [127].

1.2.2 Physiological and Biochemical Adaptation

1.2.2.1 Controlling Guard Cell Behavior and Leaf Water Status

An early response of plants to drought stress is the closure of their stomata to prevent transpiration water loss and leaf dehydration [52, 54, 154], affecting all plant water relations. The stomata closure under drought stress can result from a decrease in leaf turgor and water potential [152] or from low relative humidity of the atmosphere [156]. Under drought stress, stomata closure is considered as a first step to adapt to drought by maintaining cell turgor to continue plant metabolism [146] and to prevent the risk of losing its water transport capacity [133]. Drought stress decreased the relative leaf water content, the LWP, and the transpiration rate and concomitantly increased the leaf temperature in wheat and rice [92, 213]. Drought stress also reduced the relative leaf water content and transpiration rate in other crop species such as barley, soybean, and triticale [146, 195]. The stomatal closure and the decrease in stomatal conductance and transpiration rate under drought stress have been related to higher water-use efficiency (the ratio of dry matter produced to water consumed) in wheat [1], clover (*Trifolium alexandrium*) [143]), and alfalfa (*Medicago sativa*) [142]. Drought tolerant species improve the water-use efficiency by controlling the stomatal function to allow carbon fixation at stress and reduce the water loss [92, 236]. However, in the case of severe drought stress where plant growth and biomass accumulation are greatly diminished, the water-use efficiency is also reduced [69]. Most plants tend to show an increase in water-use efficiency when drought stress is mild [54]. Although water-use efficiency is often considered an important determinant of yield under stress and even as a component of crop drought resistance, selection for high WUE in breeding for water-limited conditions most likely leads, under most conditions, to reduced yield and reduced drought resistance [33]. Because biomass production is closely linked to transpiration, breeding for effective use of water (EUW; implies maximal soil moisture capture for transpiration, reduced nonstomatal transpiration, and minimal water loss by soil evaporation) is the most important target for yield improvement under drought stress by improving plant water status and sustaining assimilate partitions and reproductive success (HI) [33].

Stomatal closure is mediated by the plant hormone ABA [73, 163]. Biosynthesis of ABA is triggered by a decrease in soil water content and plant turgor [78]. During soil drying, ABA is synthesized in the roots and transported by the xylem to the shoot to inhibit leaf expansion and induce stomatal closure before the change in leaf water status [78, 114, 209]. ABA abundance in the xylem sap of field-grown grapevines was correlated with stomatal conductance [218]. The expression of genes associated with ABA synthesis (the 9-*cis*-epoxycarotenoid dioxygenase), *NCED1* and *NCED2*, was higher in the roots than in the leaves, especially when soil moisture declined and vapor pressure deficit increased [218]. Their expression in roots was correlated with ABA abundance in the roots, xylem sap, and leaves [218]. The results provide evidence that ABA plays an important role in linking stomatal response to soil moisture status [218].

Other hormones in addition to ABA are involved in the regulation of stomatal closure. Increased cytokinin concentration in the xylem promoted stomatal opening by decreasing the stomatal sensitivity to ABA [230], whereas the decrease in the root cytokinins was concomitant with the increase in xylem ABA and the reduction in stomatal conductance [219]. Plant hormones such as ABA, auxin, cytokinins, ethylene, and gibberellins have been shown to be involved in plant response to different environmental stresses [78, 209].

A hydraulic signaling also contributes to plant response to drought stress. Stomata respond to the rate of water loss from the leaf (evaporation demand), the change in the rate of water supply from soil, the change in xylem conductance, and to the change in leaf turgor, which can be translated to a signal to regulate stomatal aperture [43, 59, 156, 170]. The decline in root water uptake and then water potential and turgor in the leaves can lead to stomatal closure and a decrease in leaf elongation [43, 59].

1.2.2.2 Modulation of Photosynthetic Behavior Under Drought

Photosynthesis is another primary process to be inhibited by drought stress [52]. The reduction in photosynthesis under drought can result directly from stomatal and nonstomatal limitation of photosynthesis, and/or indirectly as a result of oxidative stress [53, 105, 155] (Fig. 1.1). Studies have shown that stomatal limitations could

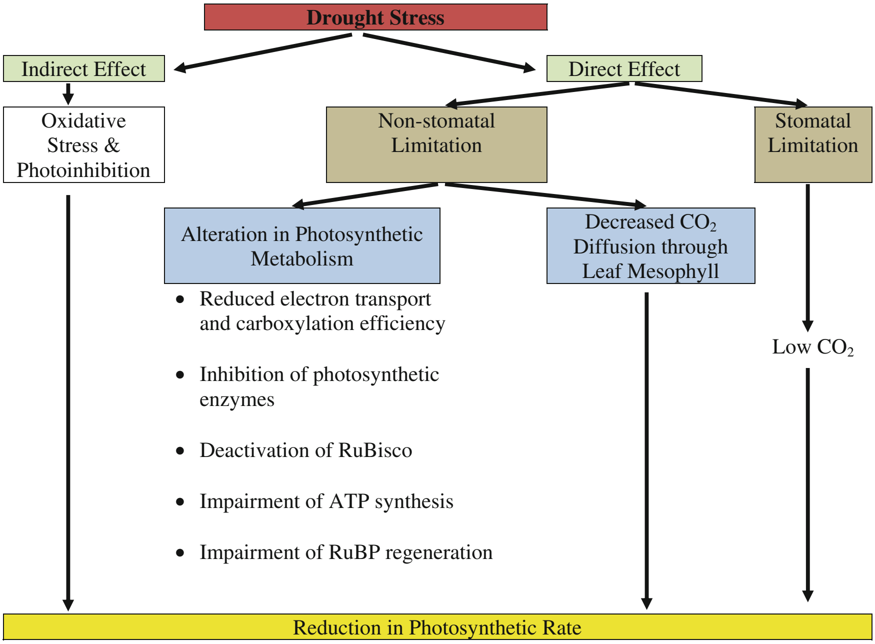

Fig. 1.1 Direct and indirect effect of drought stress on photosynthetic rate in plants. *RuBP* Ribulose 1,5 bisphosphate; *RuBisco* Ribulose 1,5 bisphosphate carboxylase/oxygenase

largely reduce CO_2 assimilation under mild to moderate drought, whereas non-stomatal limitations could account for a larger part under severe drought stress [95, 105, 116]. In stomatal limitation of photosynthesis, stomata closure occurs in response to the decline in leaf turgor and results in a decrease in CO_2 availability in the leaf intercellular air spaces [95, 96, 105].

In addition to stomatal limitation of photosynthesis, nonstomatal limitation by the decrease in CO_2 diffusion through the leaf mesophyll (a reduced mesophyll conductance) [95, 96] or alteration in photosynthetic metabolism [66, 141, 214] plays a role in determining the photosynthesis capacity under drought stress. Mesophyll conductance was depressed under drought stress [102]. The change in mesophyll conductance may be linked to alteration in the structure of the intercellular spaces due to the leaf shrinkage [141] or to the internal resistance to CO_2 diffusion in the liquid phase inside cells [103]. Other studies suggested that biochemical factors also induce changes in mesophyll conductance such as exogenous application of ABA, temperature, light, and CO_2 concentration [97, 98]. The other nonstomatal limitation of photosynthesis under drought is attributed to the alteration in photosynthetic metabolism in response to the lowered supply of CO_2 under prolonged stress [55]. These alterations in photosynthetic metabolism under drought stress include the inhibition of the photosynthetic enzymes and the synthesis of ATP and the deactivation of carboxylation enzyme RuBisco by the low intercellular CO_2 [37, 159, 191] or by the presence of tight-binding inhibitors [186]. The ATP synthesis and regeneration of ribulose 1,5 bisphosphate (RuBP) impair photosynthesis under mild drought stress [140, 141, 224]. The decrease in the activity of enzymes of the Calvin cycle has been observed in plants that are slowly exposed to a prolonged drought stress [155]. Drought stress suppresses photochemical efficiency of photosystem PSII by decreasing electron transport [150]. Meyer and Genty [160] reported that dehydration and ABA treatment decreased the electron transport rate, which was mediated by the Rubisco deactivation. Drought stress caused only small differences in the maximum efficiency of photosystem II (F_v/F_m), an indicator of the intactness of the photosynthesis electron transport [214], but had a more pronounced effect on carboxylation velocity of RuBisco ($V_{c,\max}$) in selected grassland species, decreasing the $V_{c,\max}$ of *Phleum pratense* by 20 % [214]. In addition to stomatal limitation, drought stress caused damage to photosystem II (PSII), reduced electron transport and carboxylation efficiencies of barley plants under mild drought stress [105]. Under severe drought stress, there were structural and biochemical impairment of light-dependent reactions as well as carboxylation process of photosynthesis and an acceleration of photoinhibition [105].

Stomatal limitation of CO_2 availability under drought stress could possibly lead to increased susceptibility to photodamage [66] and oxidative stress caused by the accumulation of ROS [191]. Plant mechanisms to protect the photosynthetic apparatus from the photodamage under drought are by diverting the absorbed light from photochemistry to thermal dissipation involving the xanthophyll cycle [75], or by photorespiration as suggested by its increase under drought stress [54, 124]. The rate of photorespiration in the tolerant C_3 plant *Pancratium maritimum* L. was clearly higher under moderate salt and drought stresses than under severe stresses [3]. The oxidative stress, as measured by malondialdehyde (MDA) and hydrogen peroxide (H_2O_2), was higher under severe stresses than under moderate stresses [3]. In spite of the upregulation of photorespiration under moderate stresses, the level of the oxidative stress was lower than the severe stresses because of the efficient upregulation of detoxification enzymes, catalase (CAT), and peroxidase (POD), under moderate stresses, indicating that photorespiration may not be a major contributor to the oxidative load under salt and drought stresses [3].

Photosynthetic capacity might be a factor in determining plant tolerance to water stress. Working with two cotton cultivars, TAMCO HQ95 and G&P 74 +, Gerik et al. [104] reported that the ability of HQ95 to yield more under drought stress could be due to its higher intrinsic photosynthetic capacity and carbon partitioning to the boll (higher HI). In maize, accumulated net photosynthesis across new and old hybrids was lower in drought stress treatments than well-watered treatments [174]. New maize hybrids had higher accumulated net canopy photosynthesis under drought stress and recovered faster after rehydration than old hybrids, indicating that new hybrids were more drought tolerant than old hybrids [174].

1.2.2.3 Osmotic Adjustment Through Synthesis of Osmolytes Under Drought

OA is a biochemical mechanism that helps plants tolerate water stress and saline conditions [56, 208]. In osmotic adjusted plants, the accumulation of organic solutes, known as compatible solutes, in the cell such as proline, glycine betaine, sugar alcohol, and sorbitol can improve cell hydration, maintaining cell turgor at lower water potential so the plant can survive longer and maintain metabolic processes in drying soil [27, 56, 208, 220]. Other inorganic ions mainly Na^+, K^+, Ca^{2+}, and Cl^- make a great contribution in OA by ion transport processes with related ion antiporters and ion channels [56]. Drought-stress treatments increased concentrations of phosphorus (P), potassium (K), calcium (Ca), molybdenum (Mo), manganese (Mn), copper (Cu), and zinc (Zn) in mature soybean seeds above well-watered treatment [204]. The K(+) uptake transporters 6 (KUP6) are regulated directly via an ABA signaling complex and act as key factors in OA by balancing potassium homeostasis in cell growth and drought stress responses [177]. Other regulatory processes of plant adaptation to drought stress involve control of cell OA by synthesis of osmoprotectants [7, 49]. Under various stresses, the concentration of proline in plants increased up to 80 % of the amino acid pool compared with a concentration of less than 5 % in plants under unstressed conditions [158]. Drought stress treatment increased the accumulation of compatible solutes including proline, glycine betaine, and free amino acid in *Panicum sumatrense* at 70 d after seeding compared to the control [10]. Drought stress altered sugar metabolism and increased the concentration of hexose sugars, cyclitol (scylloinositol), and proline by 3.8-, 1.5-, and 25-fold expressed on unit dry weight, respectively, suggesting that altered solute partitioning and OA may be an important factor in DT of *Ziziphus mauritiana* [60]. Gradual and severe drought reduced the concentration of sucrose in the full, rounded large seeds of soybean compared with well-watered treatment [203]. During gradual drought stress, there was a 65 % increase in bulk tissue elastic modulus (wall rigidity) coupled with OA [60]. This increase in bulk tissue elastic modulus resulted in turgor loss at the same relative water content in both stressed and unstressed leaves [60]. The OA enables plants to have a higher transpiration rate at lower LWP and to extract more water from drier soil [220]. OA also enables plants to sustain a high photosynthetic rate and expansion growth under drought stress [47]. Aside from maintaining cell hydration and turgor, organic solutes, such as proline and glycine betaine, can also assist in keeping functional macromolecules in solution, protect the cell membrane, stabilize enzymes and proteins, and protect against oxidation [18, 57, 162, 199, 215, 226, 232]. Proline plays a role as osmolyte, a reservoir of carbon and nitrogen, and has been shown to protect plants against radical-induced damage [158].

In particular crop species, OA has positively affected growth and yield under drought stress [208]. Under drought stress conditions, tolerant genotypes of sunflower had delayed wilting and maintained turgor at lower LWP than sensitive genotypes [181]. OA was observed in grass species [32] and soybean plants grown under water stress [68]. OA in wheat plants was evaluated based on plotting turgor pressure as a function of LWP in a linear slope except in the region of high water potential [164]. The results indicated that wheat cultivars with steeper slope had greater OA. The OA was greater at the tillering stage than at the heading stage for all cultivars tested [164]. It was not clear; however, whether the differences among cultivars in allocation of biomass to grain under water stress were due to OA [164]. A drought-tolerant soybean genotype PI416937 (PI) maintained turgidity during the seed-filling stage [46] and had higher transpiration and net carbon exchange rates, and higher yield [217] under drought stress. DT in the PI genotype was associated with greater mass, volume, and surface area of root [128], lower solute potential, higher pressure potential and relative water content of leaf (OA) [217], and more tolerance to high level of soil Al [112]). Genotypic variation among inbred lines of rice for the maintenance of LWP and OA under drought stress suggested that variation in OA was not related to grain yield nor yield components; however, traits contributing to the maintenance of high LWP, minimized the negative effects of water deficit on spikelet sterility, and consequently improved grain yield [134]. OA was not associated with higher yield for soybean plants grown under water stress [68]. Recent advances in biotechnology have shown that transgenic plants with a high accumulation of proline and glycine betaine had enhanced DT mainly due to protection mechanisms against oxidative stress and not necessarily caused by OA [57, 162, 226, 232].

1.2.2.4 Antioxidative Defense and Mitigation of Oxidative Stress Under Drought

Drought stress accelerates the production of ROS such as singlet oxygen ($^1O_2$), superoxide anion ($O_2^{\cdot -}$), hydrogen peroxide (H_2O_2), hydroxyl radicals ($^{\cdot}OH$), and nitric oxide (NO) [122]. Excess generation and accumulation of ROS cause oxidative damage in the apoplastic compartments and damage of cellular membranes by lipid peroxidation [22] and cause damage to proteins, carbohydrates, and DNA [106]. The production of ROS results from impairment of the electron transport process in the chloroplasts and mitochondria [106, 122]. The major sites for the production of singlet oxygen ($^1O_2$) and superoxide anion ($O_2^{\cdot -}$) in the chloroplast are photosystem I and II (PSI and PSII), whereas the major site for the generation of superoxide anion ($O_2^{\cdot -}$) in the mitochondria are complex I, ubiquinone, and complex III of the electron transport chain (ETC) [106]. The plant's strategy to reduce or prevent the damage of the ROS is to enhance and strengthen the defense mechanisms of naturally occurring nonenzymatic antioxidants (ascorbic acid, ASH; glutathione, GSH; phenolic compounds, alkaloids, nonprotein amino acids, and α-tocopherols) and enzymatic mechanisms (ROS detoxification and scavenging; superoxide dismutase, SOD; catalase, CAT; ascorbate peroxidase, APX; glutathione reductase, GR; monodehydroascorbate reductase, MDHAR; dehydroascorbate reductase, DHAR; glutathione peroxidase, GPX; guaicol peroxidase, GOPX; glutathione-S- transferase, GST; and lipoxygenase, LOX1 [106, 122, 132, 161, 240]. Alpha-tocopherol played an important protective role against drought stress in a relatively drought-tolerant genotype of barley [105]. Drought stress treatment caused an increase in activity of antioxidant enzymes such as superoxide dismutase, catalase, and peroxidase in *Panicum sumatrense* [10]. Drought stress upregulated the expression of *CAT2*, *SOD*, and *APX* genes and increased the activity of antioxidant enzymes of SOD and APX, indicating a unique pattern of activity and gene expression of the antioxidant enzymes in two barley genotypes under controlled severe drought [120]. Other researchers suggested a link between proline accumulation under stress and the quenching of singlet oxygen species [158]. Polyamines, citrulline, and several enzymes act as antioxidants and reduce the adverse effects of water deficit [92]. A drought-tolerant wheat cultivar had a higher membrane stability index (MSI), lower accumulated H_2O_2, and higher activity of antioxidant enzymes such as catalase (CAT), guaiacol peroxidase (GPX), ascorbate peroxidase (APX), and superoxide dismutase (SOD) than the drought-sensitive genotype under drought stress imposed during plant vegetative growth (18–32 d after sowing) [123]. The antioxidant defense mechanisms protect the plant cell from oxidative damage by scavenging of ROS [106]. The ROS also affects the expression of numerous genes and therefore is involved in many processes such as growth, cell cycle, programmed cell death, abiotic stress responses, pathogen defense, systemic signaling, and development [106].

1.2.2.5 Synthesis of Inducible Proteins Under Drought

Increases and decreases in protein synthesis under water stress have been reported in the literature. Although water stress resulted in an overall decline in protein synthesis, an increase in synthesis of several proteins detected by two-dimensional gel electrophoresis has been shown in soybean [29]. In maize, water stress increased the expression of 50 proteins, decreased the expression of 23 proteins, and induced 10 proteins only in the stressed plants out of 413 spots detected by two-dimensional gel electrophoresis [192]. The various proteins identified were known to be involved in plant response to water stress such as RAB17 (response to ABA) protein, and enzymes involved in metabolic pathways such as glycolysis, Krebs cycle, and lignin synthesis pathways [192] or dehydrin (dehydration-induced) proteins [62].

Proteins synthesized in response to water stress or ABA are identified as dehydrin and RAB (RAB17) proteins. Dehydrin is a family of proteins reported to be induced in response to various environmental stresses such as water, salt, cold, and ABA [27, 35, 62, 115] to reduce cellular damage [94]. Expression of dehydrin proteins (class II LEA proteins) was induced in response to water stress [38], salt [89], low temperature [171], and ABA [38]. Dehydrin proteins (DHN-5) in wheat (*Triticum durum*) have been shown to be induced by salt and abscisic acid [42]. Exposure of wheat to several stresses, such as cold, drought, and wounding, induced the expression of the dehydrin gene (*Cor410b*) by several-fold compared to the nonstressed plants [85]. Drought and salt stresses induced the expression of five *StLEA* classified as dehydrins in potato (*Solanum tuberosum*) [51]. Dehydrin proteins are present in cyanobacteria [64] and several plant species [63].

Immunolocalization studies showed that dehydrin proteins might be present in the cytoplasm [23, 166], in the nucleus [108], in the plasma membrane, or the mitochondria [35]. Dehydrin proteins were expressed in cotton during seed desiccation along with LEA proteins (LEA proteins) [119]. RAB and dehydrins are classified as class II LEA proteins [115, 144].

Many dehydrin proteins were identified as Wcs200 [222] and RAB21 [166] in rice, Wcs200 in wheat [180], G50 [48] in maize, TAS14 [110], LE4 and LE25 [41] in tomato, and CAP85 (cold and dehydration acclimated protein) in spinach leaf [171].

Dehydrins have been characterized by three major conserved amino acid sequences [62]. A highly conserved lysine-rich sequence of EKKGIMDKIKEKLPG amino acids (K segment) has been reported to exist near the carboxyl terminus of dehydrin proteins and repeated one to many times within the protein [62]. Many dehydrins contained a tract of serine residue (S segment) [62]. However, a dehydrin protein without a serine residue was characterized [65]. Another sequence of amino acid DEYGNP (Y segment) of dehydrin protein has been found near the amino terminus of many dehydrins [62]. The three sequences were called "YSK" segments [27, 62, 115].

Other characteristics of dehydrin and RAB proteins are their hydrophilic nature, resistance to denaturing by heat, lack of cysteine and tryptophan, responsiveness to ABA, and the presence of a lysine-rich sequence [35, 62, 63, 109, 166, 227]. Dehydrin proteins, detected in corn and barley seedlings in response to dehydration, were hydrophilic, glycine rich, and free of tryptophan and cysteine amino acids, and contained a conserved, repeating lysine-rich sequence of amino acids occurring twice at the carboxyl terminus and throughout the proteins [63]. Dehydrin proteins in corn and barely seedlings were similar to ABA-induced rice proteins and, to some extent, similar to cotton embryo proteins [63].

Many researchers have studied the expression of dehydrin proteins under water stress in several plant species. In soybean, dehydrin proteins (28 and 32 kDa) were detected 18 d after R_5 ($R_{5.8}$) in developing seeds from drought-stressed plants but not in seeds from the well-watered plants [207]. In the mature seeds, dehydrin proteins (28, 32, and 34 kDa) accumulated similarly in the large, round and small, shriveled seeds from drought-stressed plants as well as the well-watered plants [203, 207]. In two genotypes of barley (*Hordeum vulgare* L.), the dehydrin gene (*HvDHN1*) was upregulated at the early stage (2 d) and late stage (16 d) of drought treatment in the Rum genotype (drought tolerant genotype) and at later stages of drought (9 and 16 d) in Yarmouk genotype, but dehydrin gene (*HvDHN9*) was not expressed under drought stress at all stages of drought treatments in both genotypes [121]. Dehydration of barley and maize seedlings increased the expression of dehydrin mRNAs and induced the synthesis of dehydration-induced proteins (dehydrin proteins) [61, 63]. Polypeptides from dehydrating wheat and barley seedlings reacted immunologically with antibodies raised against maize dehydrin, indicating that dehydrin proteins were similar among grasses [61]. Water stress induced dehydrin expression in peach [17]. Transcripts of six drought-stress genes involved in essential biochemical and physiological function in plant cells were induced by drought stress in both drought-tolerant and -sensitive sunflower genotypes of sunflower but three of the six transcripts were expressed in higher levels in the tolerant genotype than the sensitive genotype [181]. Transcripts of dehydrin-like proteins (*sdi* –8) accumulated in sunflower leaves of both genotypes in response to drought stress but were at a higher level in the tolerant genotypes [181]. The expression of dehydrin genes (*dhn*, *wcor*, and *dreb*) was highly induced in leaves of the tolerant genotype of wheat under severe water stress [123]. Overexpression of the dehydrin gene (*OsDhn1*-OXs) in rice improved tolerance to salt and drought stresses via scavenging ROS [139]. The overexpression of a wild chickpea (*Cicer pinnatifidum*) dehydrin in tobacco plants had positive effects on their dehydration tolerance [27]. Subjecting two maize (*Zea mays* L.) genotypes, with contrasting sensitivity to dehydration, to moderate drought condition caused upregulation of protective and stress-related proteins (mainly chaperones and dehydrins) in both the sensitive and tolerant genotypes, but the number and levels of upregulated protective proteins were generally lower in the sensitive genotype [28]. The results indicated that the sensitive genotype had a reduced level of photosynthesis as indicated by specific changes in the components of the translation machinery [28]. Cryotolerant species such as wheat and rye accumulate more heat-stable dehydrins than cryosensitive species such as maize [35].

Regulation of gene expression by ABA suggests that ABA may have a role regulating the plant response to dehydration [72] and in mediating the DT in plants [50]. Under water deficient conditions, ABA regulated the expression of a group of drought-induced genes [41]. Dehydrin-like proteins in pea seedlings were induced in response to ABA [23]. In contrast, the expression of dehydrin and LEA proteins in developing seeds might not be regulated by ABA [193]. Expression of RAB/dehydrin proteins in the immature embryo of barley in response to an osmotic stress imposed using mannitol was independent of the ABA pathway [88]. Two ABA-response proteins, ABR17 and ABR18, were synthesized in *Pisum sativum* seeds during desiccation [26]. Characterization of the two proteins revealed that they were similar in amino acid composition and 56 % identical in their N-terminal sequence, but the two proteins had no homology in their N-terminal sequence to any of the LEA or dehydrin proteins [26]. Several factors such as developmental stages, hormones, and dehydration, can regulate the expression and activities of LEA proteins including dehydrins [51]. Dehydrins mRNA (DHN14) rapidly accumulated in winter wheat in response to drought and ABA [58]. In an investigation on sunflower (*Helianthus annuus* L.), the relationship between abscisic acid and accumulation of a dehydrin mRNA (*HaDhn1a*) has shown that there are two regulation pathways of *HaDhn1a* transcript accumulation, an ABA-dependent and an ABA-independent one, which may have cumulative effects [107].

A proposed role of dehydrins, LEA, RAB, and other stress proteins has been in protecting cells from dehydration stress [17, 39, 61, 83]. The highly conserved lysine-rich sequence (K segment) within dehydrin proteins forms a secondary structure (an amphiphilic α helix), which suggests that the K segment is an essential part for dehydrin function under dehydration stress [63, 83, 84, 111, 194]. The hypothesized role for the K segment of dehydrin is to form a hydrophobic interaction with DNA [109], partially denatured proteins, and damaged membranes, thus acting as a chaperone to stabilize protein folding under dehydration [62, 94, 109]. It has been supposed that dehydrin's function is to stabilize proteins in the membrane or in the matrix of the mitochondria [35]. Although dehydrin proteins are hydrophilic proteins, G50 (dehydrin protein) in maize was able to form a hydrophobic interaction in vitro [48]. Dehydrin may also have a role similar to compatible solutes (such as proline, sucrose, and glycine betaine) in OA. Another possible role of dehydrins is to bind with the accumulated ions (ion sequestering) under water stress and to control solute concentration in the cytoplasm [82]. Dehydrin may have a cryoprotective role in macromolecular stabilization by binding water molecules on their hydrophilic surfaces which reverses or prevents further denaturation of cellular proteins [45, 62]. Maturation proteins, which were induced in response to ABA or dehydration, might protect the plant under stress by stabilizing cell membranes [83]. Evidence from biochemical assays and localization experiments suggests multiple roles for dehydrins, including membrane protection, cryoprotection of enzymes, and protection from ROS [115].

1.3 Molecular Adaptation Under Drought Stress

1.3.1 Signaling Pathway Under Drought and Their Crosstalk

Plant tolerance to drought stress is triggered by complex multicomponent signaling pathways to restore cellular homeostasis and promote survival [113] (Fig. 1.2). The plant phytohormone abscisic acid plays a role in plant response to drought and DT by activating stress-responsive genes and regulating stomatal conductance [179,

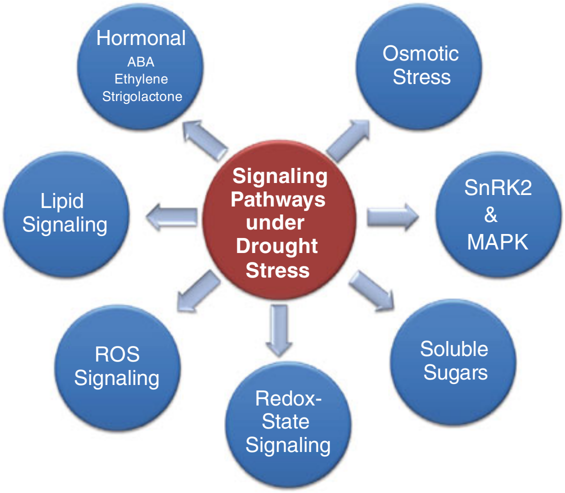

Fig. 1.2 Signaling pathways under drought stress. *ROS* Reactive oxygen species; *SnRK2* Sucrose nonfermenting 1-related protein kinase 2; *MAPK* Mitogen-activated protein kinase

231] and has a vital function as a growth inhibitor [71]. The ABA is synthesized de novo in response to drought stress, which induces the expression of 9-*cis* epoxy-carotenoid dioxygenase (NCED) gene involved in ABA biosynthesis in *Arabidopsis* [131]. Transgenic *Arabidopsis* plants overexpressed *AtNCED3* gene increased the endogenous ABA, increased the transcription of drought- and ABA-inducible genes, showed a reduction in transpiration rate from leaves, and enhanced DT [131]. The ABA triggers the transcriptional changes in genes related to carbohydrate and lipid metabolism, indicating its function at the interface of plant response to stress and cellular metabolism [125]. Exogenous application of ABA could effectively alleviate damages caused by multiple abiotic stresses, including drought, salt, heat, and cold by inducing the accumulation of osmoprotectants and antioxidants, keeping cell membrane integrity, increasing photosynthesis, and keeping ion homeostasis, which protected Bermuda grass from damages caused by abiotic stresses [49]. Previously, ABA was thought to be a long-distance messenger of stress traveling from roots to shoot [179]. However, recent studies have shown that ABA is produced in the veins of the leaves themselves, where it acts on nearby stomata, as well as in the specialized "guard" cells, which close and open the stomata [179].

The abscisic acid signal is perceived by different cellular receptors [113] (Table 1.1). Recent research suggested that there are three cellular ABA receptors: nucleocytoplasmic [153, 184]; plasma membrane [183]; and chloroplast (receptors) [79] (Table 1.1). The ABA binds with the nucleocytoplasmic receptor (PYR/PYL/RCARs), which inhibits the type 2C protein phosphatases (PP2Cs) [153, 190] (Fig. 1.3). Inactivation of PP2Cs activates accumulation of active sucrose nonfermenting 1-related protein kinase 2 (SnRK2 s; [153, 190]). The SnRK2 s regulates ABA-responsive transcription factors (AREB/ABF; ABA-responsive element binding protein/ABRE-binding factor) [two basic leucine zipper (bZIP) transcription factors] by binding with the ABA-responsive *cis* element (ABRE) of the ABA-regulated genes [234]. Other transcription factors such as MYC, MYB [2], RD26, and NAC [101] are involved in the induction of drought-inducible genes mediated through ABA-dependent pathway (Fig. 1.3).

In addition to the ABA-dependent pathway, the drought stress signal is mediated through an ABA-independent pathway (osmotic stress signal) to regulate the

Table 1.1 ABA cellular receptors

Cellular compartments	Receptors	Name	References
Nucleocytoplasmic	PYR/PYL/RCARs	PYR Pyrabactin resistance PYL Pyrabactin resistance like RCARs Regulatory component of ABA receptors	[153, 184]
Plasma membrane	GTGs (GTG1/GTG2)	G protein-coupled receptor-type G protein	[183]
Chloroplast	CHLH/ABAR	H subunit of Mg-chelatase	[79]

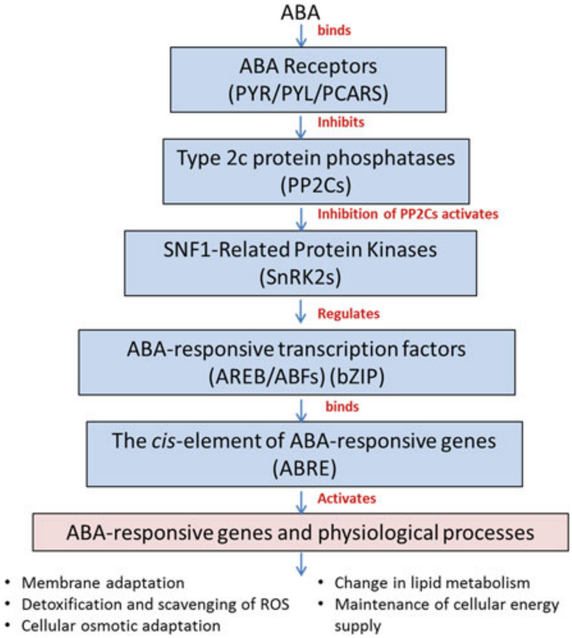

Fig. 1.3 ABA signaling pathways in regulating ABA-responsive genes and physiological processes

expression of different drought-inducible genes [54, 211] (Fig. 1.4). Transcription factors DREB1/CBF and DREB2 (belonging to AP2/ERF transcription factors) bind with the *cis*-acting element DRE/CRT (dehydration-responsive element/C-Repeat) of the drought-inducible genes and induce the expression of the DT genes [148, 211, 233]. DREB and ERF proteins regulated the expression of wheat (*Triticum durum*) dehydrin gene (*TdCor410b*) through a single functional C-repeat (CRT) element [85]. Another ABA-independent pathway regulating the dehydration response is through a transcription factor identified as NAC which binds with the *cis*-element of the drought-inducible gene (*ERD1*) [216, 225] (Fig. 1.4).

Recently, Ha et al. [118] reported that the hormone strigolactone positively regulates drought response and tolerance in *Arabidopsis*, reporting a new signaling pathway. The synthesis of strigolactone is controlled by a more axillary growth (Max) gene family [118]. *Arabidopsis* plants with Max mutant genes were more sensitive to drought- and salt-stress compared with the wild types and exhibited increased stomatal density, increased leaf water loss rate, and slower ABA-induced stomatal closure, suggesting that strigolactone acts by regulating stomatal transpiration rate [118]. They also suggest that strigolactone and ABA interact and play an important role in integrating stress signals to stomatal development and function [118].

Current models emphasize the function of ROS as a signaling interface in plant drought and salt adaptation that links stress signals to regulation of metabolism and cellular energy balance (ROS signaling) [15, 113] (Fig. 1.2). The transcription factor (*WRKY*) is suggested to be involved in linking osmotic and oxidative stress

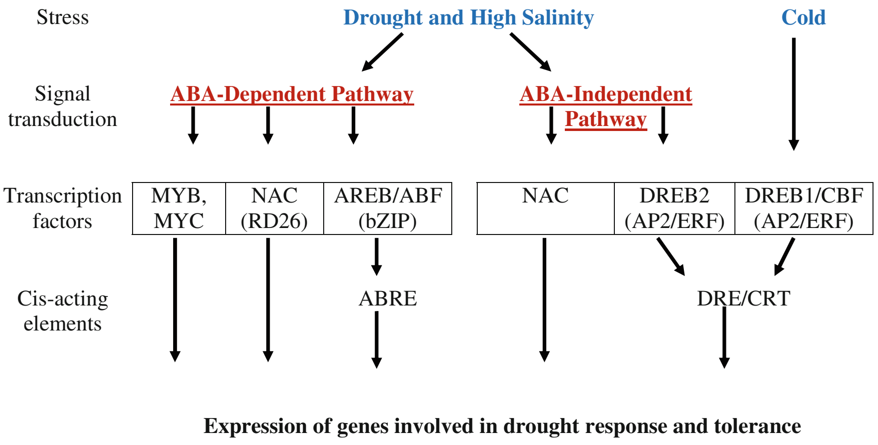

Fig. 1.4 Transcriptional regulatory networks of abiotic stress signals and gene expression. There are three ABA-dependent and three ABA-independent pathways. In the ABA-dependent pathway, the transcription factors (MYB, MYC, NAC, and AREB/ABF) function in ABA-inducible gene expression. AREB/ABF binds with the *cis*-acting element (ABRE) of the ABA-inducible genes. In the ABA-independent pathway, the transcription factors (NAC, DREB1/CBF, and DREB2) function in this process. The DREB1/CBF and DREB2 bind with the *cis*-acting element (DRE/CRT) of the ABA-independent stress inducible genes. Modified from Shinozaki and Yamaguchi-Shinozaki [211] with permission of Oxford University Press

defense and in ROS-mediated signaling crosstalks [113]. The transcription factor of *WRKY33* controls genes that function in detoxification of ROS such as glutathione *S*-transferase (*GSTU11*), peroxidases, and lipoxygenase (*LOX1*) in *Arabidopsis* [132]. The transcription factor *ThWRKY4* controls the genes related to ROS scavenging such as superoxide dismutase and peroxidase in *Tamarix hispida* [240]. These data suggest that the transcription factor *WRKY* has a role in controlling cellular ROS levels in abiotic stress signaling. Plants with overexpression of *ThWRKY4* were referred to *ThWRKY4*-mediated cellular protection against toxic ROS levels [240]. Recent advances suggest that there is a crosstalk of ROS signaling with other stress-triggered hormonal signaling such as ABA and other endogenously induced redox and metabolites signaling [113].

Increasing evidence indicates that lipid signaling is an integral part of the complex regulatory network in plant response to drought and salinity [167, 197] and is involved in primary sensing of abiotic stresses and in triggering and regulating cellular hormonal signaling [113]. Modification of lipids produces different signaling messengers such as phosphatidic acid (PA), diacylglycerol-pyrophosphate (DAG-PP), and phosphoinositides [36]. The production of PA, the key lipid messenger in plant response to environmental stresses, is regulated by phospholipase D (PLD) [126]. The activity of PLD in plants increases in response to abiotic stress such dehydration, drought, and salinity [126]. Recent studies indicated that PLD and PA play an important role in plant drought and salt stress tolerance [25, 151]. PLDα1 promotes stomatal closure and reduces water loss [126, 151]. PA binds with

PP2C (a protein phosphatase 2c; ABI1, ABA-insensitive 1) and inhibits the negative effect of PP2C in the ABA signaling pathway, thus promoting the ABA effect on stomatal closure [239], indicating that the modification of cellular lipid (through the biosynthesis of PA by *PLDα*) is essential for regulating abiotic stress-related ABA signaling [113, 151]. Introducing Arabidopsis *PLDα* under the control of a guard-cell–specific promoter $AtKatl_{pro}$ into two canola (*Brassica napus*) cultivars ($AtKatl_{pro::}$ *PLDα*) decreased water loss and improved biomass accumulation under drought and salt stresses in canola [151]. These results support the evidence of the involvement of lipid signaling in plant response to drought and DT.

Other signal pathways trigger plant response to drought stress such as SnRK2 (sucrose nonfermenting 1-related protein kinase 2) and MAPK (mitogen-activated protein kinase) signaling, possibly stomatal signaling [113, 145], soluble sugars (namely sucrose, glucose, and fructose) signaling [55], and redox-state of the photosynthetic electron components and the redox active molecules acting as regulatory agents [99] (Fig. 1.2).

1.3.2 Activation of Transcriptional Factors Under Drought

As indicated in the previous section, drought stress induces the expression of DT genes through ABA-dependent and -independent pathways. There are four major transcription factors involved in the regulatory network in plant response to drought, cold, and heat stresses [169] (Table 1.2). AREB/ABFs are bZIP transcription factors that regulate ABA-dependent gene expression under osmotic stress by binding with the *cis*-element of the ABA-responsive (ABRE) gene expression [157]. The transcription factors DREB1/CBF and DBEB2 in *Arabidopsis* regulate ABA-independent gene expression by binding with the *cis*-element of DRE/CRT of drought-responsive genes [5, 6, 148]. Other transcription factors (NAC genes) have been identified in *Arabidopsis* and rice that have important functions in stress responses [168]. The NAC transcription factors (SNAC group) bind with the

Table 1.2 Major transcription factors for abiotic stress-responsive gene expression to improve drought tolerance

Abiotic stress	Transcription factors	*Cis*-acting element of stress-responsive gene	References
Osmotic (ABA-dependent)	AREB/ABF	ABRE	[157]
Cold	DREB1/CBF	DRE/CRT	[130, 148]
Osmotic and Heat	DREB2	DRE/CRT	[87, 149, 200]
Drought	NAC	NACR	[168, 223]

NACR (NAC recognition sequence) of the stress-responsive genes in *Arabidopsis* [168, 223]. The drought-response transcription factors such as AREB/ABF, DREB1/CBF, DREB2, and NAC function in DT and in transcriptional regulatory networks and crosstalk in abiotic stresses including drought, salt, cold, and heat [87, 149, 169, 200]. The *TaWLIP19* (wheat version of bZIP), *TaWRKY10*, *TaMYB33*, and *TaNAC69* transcription factor genes were induced in *Triticum aestivum* and *Triticum turgidum*, indicating the involvement of these transcription factors in drought stress responses [24].

1.3.3 Drought Induced Genes and Their Expression in Transgenic

Molecular analysis using microarray identified the drought-inducible genes [211, 212]. The products of these genes in *Arabidopsis* and rice were classified into functional and regulatory proteins [189, 212]. The functional proteins include those proteins involved in abiotic stress tolerance such as protection factors of macromolecules (such as LEA proteins, chaperones, and dehydrins), detoxification enzymes, enzymes for the biosynthesis of osmolytes (proline and sugar), water channel transporter, and proteases. The regulatory proteins include transcription factors (DREB2, AREB, MYB, MYC, bZIP, and NAC), protein kinases, phosphatases, lipid metabolism, and ABA biosynthesis.

With the advancement of biotechnology and increasing genomic tools, the transgenic approach has become an attractive strategy for genetically engineering plants for improving DT [138, 229, 238]. Molecular control mechanisms of the transgenic plants for stress tolerance are based on activation, regulation, or overexpression of specific drought-related genes [229]. These genes are either functional proteins (osmolyte synthesis enzyme, raffinose oligosaccharides biosynthesis enzyme, dehydrin proteins, key photosynthetic enzymes, ROS detoxification and scavenging enzymes), or regulatory proteins (signaling and transcriptional factors) [7, 211, 212, 229]. In the last decade, several attempts using genetic engineering have been made to enhance plant tolerance to drought through producing transgenic plants with a “single-function” gene as well as a transcription factor for abiotic stress tolerance [7]. Because the tolerance to abiotic stress in nature is controlled by many genes; the recent trend is shifting towards genetic transformation of multiple genes or transcription factors [7].

Transgenic plants with expressed functional proteins improved DT. Transgenic soybean expressing *AtP5CR* gene (encoding L-Δ1-Pyrroline-5-carboxylate reductase) had higher relative water content and enhanced DT [74]. Wheat plants transformed with the *Vigna aconitifolia* [Delta (1)-pyrroline-5-carboxylate synthetase (P5CS) cDNA that encodes the key regulatory enzyme in proline biosynthesis] showed an increase in the accumulation of proline and enhanced tolerance to drought mainly due to protection mechanisms against oxidative stress and not caused by OA [226]. Proline accumulation in other transgenic plants acts as a component of antioxidative defense and enhanced DT [162, 215, 232]. Transgenic *Arabidopsis* plants with the *Go1S* gene (encoding galactinol synthase, a key enzyme involved in raffinose oligosaccharides biosynthesis) was shown to enhance DT [221]. Transgenic rice plants with overexpression of the dehydrin gene (*OsDhn1*-OXs) showed an enhanced tolerance to drought and salt stress as indicated by the chlorophyll fluorescence (Fv/Fm), fresh and dry weight, water and chlorophyll content, and survival ratio, and had an increased tolerance to oxidative stress and maintained a relatively low level of H_2O_2 under salt and drought stress as compared to wild-type plants [139]. Transgenic plants of *Arabidopsis thaliana* with ectopic expression of dehydrins (Dhn-5) exhibited stronger growth under high concentrations of NaCl or under water deprivation, and showed a faster recovery from mannitol treatment, had more negative water potential, higher proline contents, and lower water loss rate under water stress compared to wild-type plants [42]. Transgenic plants with Dhn-5 had an improved tolerance to salt and drought stress through OA [42]. Plant adaptation to drought stress can be markedly improved in tomato (*Solanum lycopersicum* L.) by overexpression of the cell wall invertase (cwInv) gene *CIN1* (a key enzyme regulating sink activity and playing a role in plant growth and development) from *Chenopodium rubrum* [12]. Transgenic plants with *CIN1* overexpression reduced water consumption by limiting stomatal conductance during the drought period, whereas photosynthetic activity was maintained, delayed senescence, leading to higher water use efficiency and improving DA strategy [12]. *CIN1* overexpression was accompanied by the increase in the concentrations of the senescence-delaying hormone trans-zeatin and the decrease in the senescence-inducing ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC) in the leaves [12].

Improvement in photosynthetic capacity under drought stress can be achieved by engineering transgenic plants with the overexpression of the genes of a key C_4 photosynthetic pathway to C_3 plants. Two transgenic rice lines were produced by overexpression of the maize-specific pyruvate orthophosphate dikinase (PPDK) independently or in combination with maize-C4–specific phosphoenolpyruvate carboxylase (PCK) [117]. Transgenic rice lines had an increased leaf photosynthetic rate, higher leaf water content, stomatal conductance, transpiration efficiency, and root oxidation activity, and a stronger active oxygen scavenging defense than the untransgenic line (wild type) under well-watered and drought-stress treatments [117].

Transgenic plants with overexpressed genes coding antioxidant enzymes showed enhanced tolerance to drought stress. Transgenic tobacco plants with cytosolic Cu/Zn-superoxide dismutases (SOD) from *Oryza sativa* showed enhanced tolerance to oxidative stress and enhanced tolerance to salt, water, and polyethylene glycol (PEG) stresses as measured by net photosynthesis over the wild type [21]. These results suggested that the overexpressed Cu/Zn-SOD enhanced the chloroplast antioxidant system [21]. Developing transgenic tobacco plants overexpressing *Arabidopsis thaliana* Monodehydroascorbate reductase (MDAR gene; *AtMDAR1*) exhibited higher MDAR activity and a higher level of reduced ascorbate (AsA) compared to nontransformed control plants [86]. The transgenic plants showed enhanced stress tolerance in term of significantly higher net photosynthesis rates under ozone, salt, and PEG stresses [86]. Tobacco (*Nicotiana tabacum* L.) plants transformed and constitutively overexpressed with the *Arabidopsis thaliana* gene for ascorbate peroxidase 3 (APX3) exhibited greater photosynthetic capacity, higher fruit number, and seed mass [235].

Overexpressing regulatory proteins in transgenic plants has also shown an improvement in DT. Transgenic *Arabidopsis* with overexpression of *AtNCED3* gene (9-*cis*-epoxycarotenoid dioxygenase enzyme involved in ABA synthesis) had an increase in endogenous ABA level, higher transcription of drought- and ABA-inducible genes, lower transpiration rate, and enhanced DT [131]. Overexpression of the DREB1/CBF transcription factor in transgenic plants increased stress tolerance to drought, freezing, and salt stresses [148]. Overexpression of the rice gene OsDREB1A transcription factor (homologues of DREB1/CBF) in *Arabidopsis* resulted in stress-responsive gene expression and stress tolerance [80]. Similarly, overexpression of the rice transcription factor gene OsDREB1 or *Arabidopsis* transcription factor gene (DREB1) enhanced drought and chilling tolerance in rice [130]. Overexpression of ABF3 or AREB2/ABF4 transcription factor genes increased the sensitivity to ABA, reduced transpiration rate, and improved the DT of *Arabidopsis* [135]. Overexpression of *AP37* (subgroup of AP2 transcription factor) in rice under the control of the constitutive promoter *OsCc1* (the *OsCc1*:*AP37* plants) significantly enhanced DT in the field, which increased grain yield by 16–57 % over controls under severe drought conditions, yet exhibited no significant difference under normal growth conditions, suggesting the *AP37* gene has the potential to improve DT in rice without causing undesirable growth phenotypes [176]. Overexpression of the Arabidopsis HARDY gene [belongs to the stress-related AP2/ERF transcription factor (APETALA2/ethylene responsive element binding factors)] in *Trifolium alexandrinum* L. (transgenic plants) improved the instantaneous WUE under drought stress by reducing transpiration (E), improved the growth of drought-stressed transgenic plants by delaying water depletion from soil and preventing rapid decline in photosynthesis (A), and significantly increased the transgenic plant fresh and dry weights under the combined drought and salt stresses in the field compared to the wild-type plants [4]. The results proved the efficiency of overexpression of a single gene in improving tolerance to abiotic stress under field conditions [4].

Recently, *Arabidopsis* plants were engineered with a modified ABA receptor [Pyrabactin Resistance 1 (RYR1)] that can be activated by a common agrochemical fungicide (mandipropamid) [185]. The transgenic plants with re-engineered receptor can withstand 12 days of water withholding and survive after being rewatered when plants are sprayed with mandipropamid agrochemical compared with the control plants (wild type). This result demonstrated that mandipropamid was efficient in controlling ABA responses and DT [185].

1.4 Concluding Remarks

Plant responses to drought are complex interacting processes including morphological, physiological, biochemical, and molecular changes that allow plants to cope with drought stress. Plant strategies to cope with drought can be through escape, avoidance, or tolerance. The contribution of each of these strategies for drought resistance varies among species and interacts with environmental conditions and depends on many factors. In the escape mechanism, plants end their life cycle before the onset of drought stress at the end of the growing season, which results in earlier maturity and in most cases lower yield to survive the terminal drought stress. In the avoidance mechanism, two important processes are involved: plants uptake more water from the soil and conserve moisture by regulating the stomatal aperture to maintain leaf water hydration. In the last strategy, plants trigger mechanisms to withstand water dehydration including OA, accumulation of dehydrins, scavenging the ROS, repairing the damage in proteins and membranes. To regulate these responses, drought signaling pathways are involved in mediating the expression of many drought-responsive genes. These pathways include hormonal signals (such as ABA, ethylene, and strigolactone), ROS signal, lipid-derived signal, soluble sugar signal, and others. These signaling pathways are either ABA-dependent or ABA-independent. These signal pathways are crosstalk in mediating plant responses to drought and other stresses. Major transcription factors such as ABREB/ABF, DREB1/CBF, DREB2, and NAC play important roles in the crosstalk of these signaling pathways. Drought stress regulates expression of many drought-responsive genes including functional proteins (such as osmolyte, antioxidant enzymes, and dehydrins) and regulatory proteins (such as transcription factors). In the last decade, many studies have been done to transfer a single or multiple genes from one plant to another or overexpressing them in the same plants to produce transgenic plants. Transgenic plants have shown enhanced DT and can be a promising tool for further understanding the functions of these drought-responsive genes in plants under drought stress. Researchers reported that transgenic plants with overexpressing genes encoding to photosynthetic enzymes, osmolyte synthesis, dehydrins, antioxidant enzymes, enzymes involved in ABA synthesis, ABA receptors, and enzymes involved in source-sink regulation have shown improved DT. Because drought stresses in the field are very complex phenomena involving many interacting factors and coincide with many other stresses, future research is needed to focus on the transfer of more than one gene and to test these transgenic lines under natural growing conditions in the field.

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