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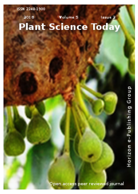

Review Article

An insight into drought stress and signal transduction of abscisic acid

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Abstract

The sustainable crop production is one of the major issue in the era of urbanization, industrialization, and globalization. In the environment, there are number of abiotic and biotic factors which are hampering the sustainable production of crops. The drought is one of the constraints which directly/indirectly affects the crop yield. It has various negative effects on the normal physiology and biochemistry of the plants. Therefore, researchers must have to work in the field of developing drought-tolerant crop plants to meet the food needs of the exponentially growing population of the world. The present study is the outcome of an extensive literature survey on the basic perturbations of drought to the crops, role of abscisic acid (ABA) in stressful conditions and its signal transduction.

Keywords

Drought stress; physiological consequences; ABA-dependent signaling; ABA-independent signaling; drought tolerance.

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Introduction

Drought is a period with low average precipitation leading to prolonged shortage of water in a given area. According to Mishra and Cherkauer (2010), the shortage in precipitation is coupled with the higher rate of evapotranspiration which results into the agricultural drought (1). The agricultural drought is lack of sufficient moisture content in the soil to meet the normal growth and development of plants (2). There are number of factors that cause reduction in the yield of crops but drought is the most frequent factor related to the reduced production of crops (3). Therefore, efforts should be made to improve the crop yield by 40% by 2025 in those areas where water is limiting factor (4). In 2018, the world population is 7.6 billion, by 2025 it is expected to increase to 8.5 billion and in 2050 the world population will be 9.7 billion (UNDESA, 2015) (5). The major challenge to the present crop system is to increase the crop production to create sufficient food to feed the increasing population and to reduce the number of starving people by 50% (6). In plants, the drought affects the basic biochemical and physiological processes like photosynthesis, respiration, nutrient metabolism, ion uptake capacity etc. which are directly associated with the productivity of the plants (7, 8). The consequences of drought stress vary at cellular level with respect to plant species, stress duration, stage of plant development etc. (9). It was reported that sometime severe drought can even arrest the photosynthesis and lead to plant death (10).

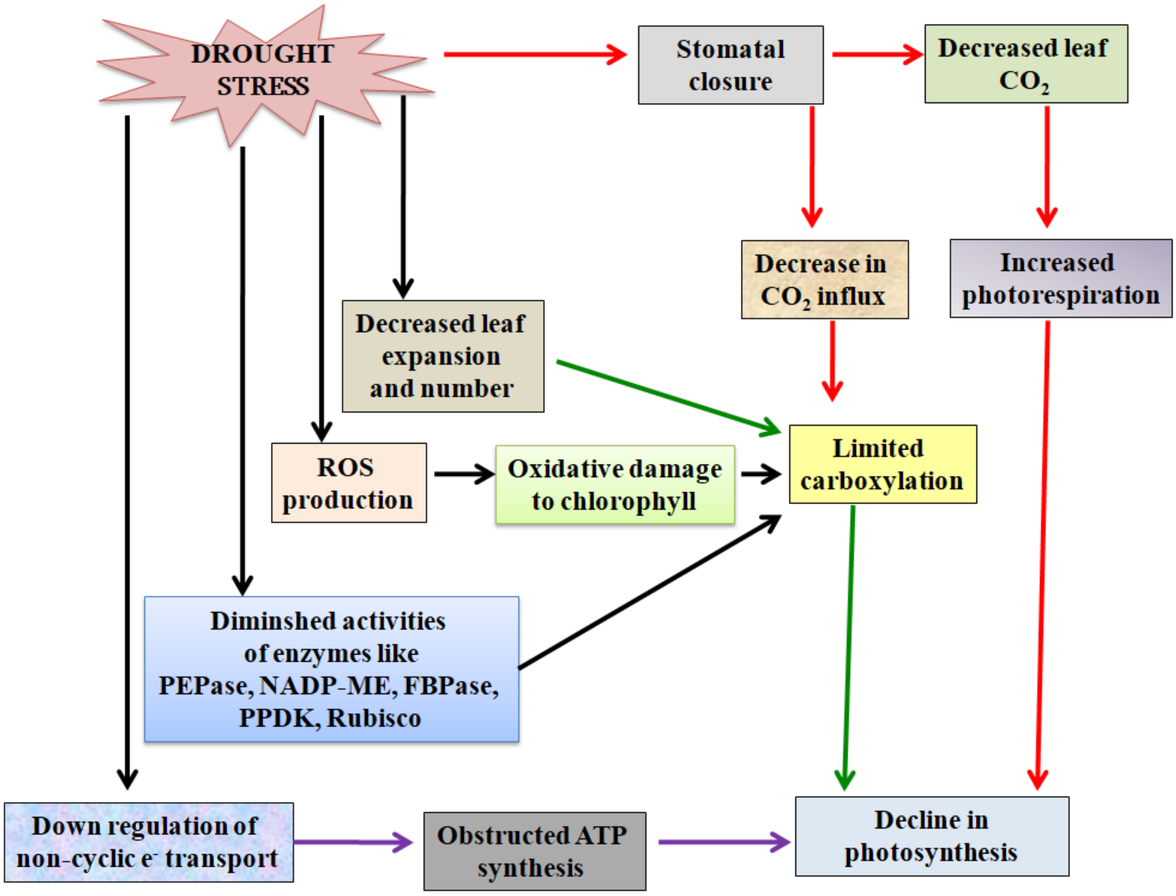

Fig. 1. The consequences of plant to drought stress (15)

Therefore, the development of drought-tolerant plants is the need of the hour to the areas which are at risk of frequent drought.

Areas of world under the risk of severe drought

Some of the areas of world which are facing severe drought are Cape Town, Malawi, Somalia of South Africa, Italy and Spain in Europe, Southern and Eastern part of India, Bangkok in Thailand etc. (11, 12).

There are number of other areas which are at the risk of severe drought. The plant are the very first recipients of any stress because of their immobility. Therefore, it is very essential to understand the basic phenomenon occurring in plant during such conditions.

Drought stress induced consequences among plants

The drought during any stage of plant life cycle can result in different morphological, physiological and biochemical consequences in plants and few of them are discussed as follows (Fig. 1):

i. Reduced plant growth and development: The very first and foremost effect of drought is reduced germination and seedling establishment (13). In most of the crops, the germination is reported to reduce under drought stress. The growth of any plant is dependent upon division, elongation, and differentiation of the cells. The drought is reported to reduce turgor pressure of cell which is directly associated with the cell division (14). Drought is also found to affect the crop phenology (*i.e.* the different growth and developmental aspects of the plant with respect to time) (15). Moreover, drought stress can trigger the early switching of plant developmental stage *i.e.* a plant can enter early from its vegetative phase to reproductive phase (16).

ii. Disturbance in plant water relationship: The plant water relation includes relative water content (RWC), water potential, osmotic potential, pressure potential, and transpirational rate (TR) (9, 17). These all indices associated with plant water relation are greatly affected by reduced content of water in the soil. It was reported that in the crop plants, the decrease in RWC, TR is coupled with the increase in leaf temperature (18).

iii. Impaired nutrient uptake and assimilation: The nutrients come from the internal cycling of reserve material which is essential for plant growth and biomass accumulation (19). According to Gutierrez-Bemand and Thomas (1999) the absorption of nutrients depends upon absorption kinetics of nutrients, soil nutrient supply, morphology and growth of roots (20). During water deficit, the nutrient supply gets decreased because of slow diffusion of nutrients due to the

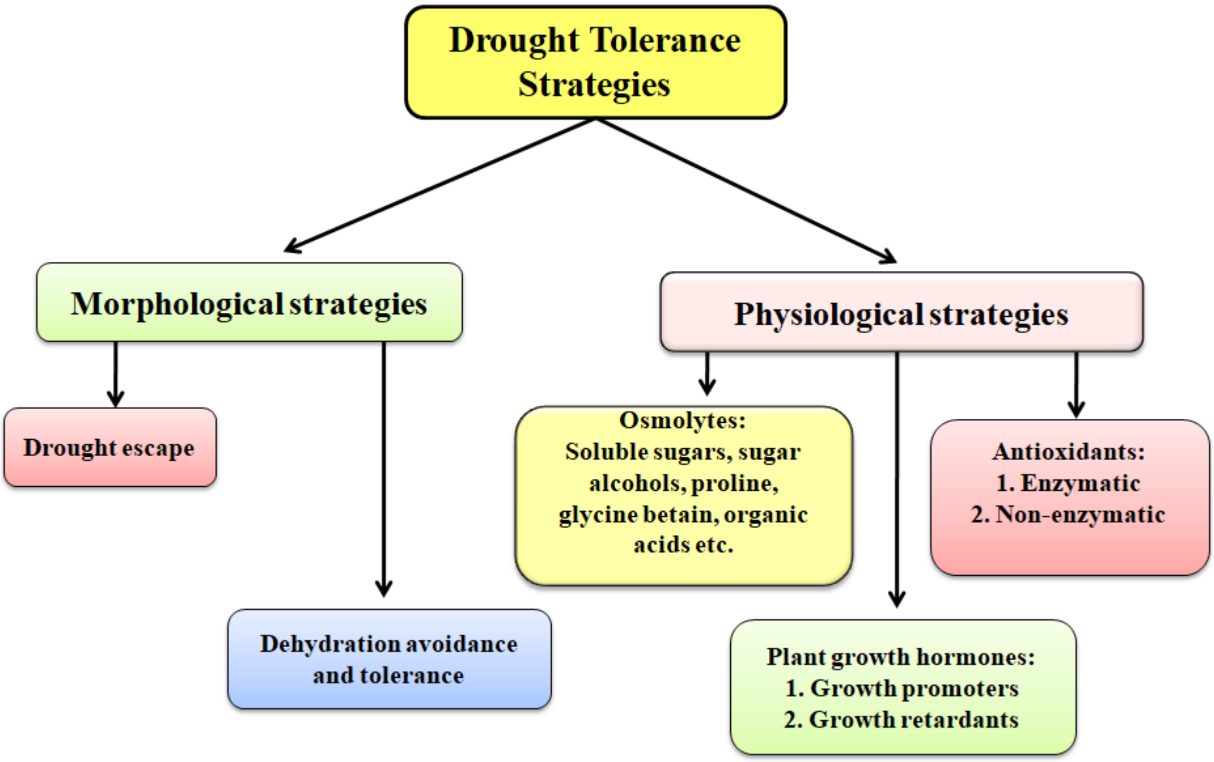

Fig. 2. Morphological and physiological strategies adopted by crop plants during drought stress

decline in soil-water potential (9). The reduced TR is associated with disturbed nutrient uptake to some extent. It may occur because of the limited energy available for the assimilation of NO_3^-/NH_4^+, PO_4^{3-}, and SO_4^{2-} and alteration in membrane permeability (21, 22).

iv. Oxidative damage: Generally, in plants under abiotic stress the generation of reactive oxygen species (ROS) takes place. The ROS includes superoxide anion, hydroxyl radicals, hydrogen peroxide, alkoxy radicals, and singlet oxygen that are responsible for number of injuries in plant cell (23).

There are number of other consequences also reported during drought stress like disturbed respiration, ATP synthesis, photosynthesis etc.

Drought tolerance strategies adopted by plants

Due to sessile nature of plants or anchored in one place during abiotic/biotic stress; plant adopt various morphological and physiological strategies for their survival which are as follows (Fig. 2):

1. Morphological strategies: The morphological strategies include drought escape and dehydration avoidance by some morphological modifications.

i. Drought escape: When a plant completes its life cycle/becomes dormant before the onset of the drought then this ability of plant is referred as drought escape. Drought escape is generally observed in some plants growing in desert areas. The life cycle of these plants is extremely short as compared to others and for further propagation of them, they produce seeds during short rainy seasons (24).

ii. Avoidance of dehydration: During scarcity of water if a plant is able to maintain its normal plant water content/cellular hydration or by minimizing water loss through transpiration (25) is referred as dehydration avoidance. For this, plants undergo some morphological modifications to minimize stress-induced consequences. Crops plants were reported to extract more water during drought from the soil so that they can better resist against drought (26). The root plasticity is another important characteristic of a genotype to regulate the growth pattern root accordingly (27). The deeper root system, more root proliferation, root length density are considered drought avoidance traits among plants (26, 28, 29) and crop genotypes with more root growth are preferred in drought prone areas.

2. Physiological strategies: The plants under drought stress generally adopt physiological adaptations such as osmotic adjustment, roles of plant growth regulators (PGRs) and antioxidative defense system in minimization of damages/injuries.

i. Osmotic adjustment: According to Serraj and Sinclair (2002) the osmotic adjustment is accumulation of such organic/inorganic solute (osmolytes) in cell during stress which are helpful in maintaining lower water potential in cell without declining actual water content thus, drives water from soil (30). The commonly reported osmolytes during drought stress are proline, soluble sugars, glycine betaine (GB), organic acids, trehalose etc. (9) and osmolytes are also called as compatible solutes. They maintain the turgor pressure of cell and promote water uptake of roots without causing any harmful effects.

ii. Role of PGRs: The main PGRs are auxins, gibberlins, cytokinins, ethylene and abscisic acid (ABA). From these gibberlins and cytokinins promotes the growth of plant, while ethylene and ABA produce growth retarding effects (33). It was observed that during stress the concentration of growth retarding PGRs get increased and growth promoting PGRs decreased to cope up with the stress.

iii. Role of antioxidative defense system: The stressful conditions enhanced the generation of reactive oxygen species (ROS) in plant and ROS affect the plant's biochemical and physiological processes *via* oxidative damage to lipids of membrane, proteins, other macromolecules of cell. The antioxidative defense system regulate the ROS induced damage by its enzymatic and non-enzymatic components (34). The enzymatic components include superoxide dismutase (SOD), catalase (CAT), guaiacol peroxidase (GPX), ascorbate peroxidase (APX), glutathione reductase (GR), while non-enzymatic components include ascorbic acids, compatible solutes, α-tocopherol, β-carotene, zeathanxin etc. The protective action of antioxidative enzymes against ROS are explained as follows (35):

a. $O_2^- + O_2^- + 2H^+ \xrightarrow{SOD} H_2O_2 + O_2$

b. $H_2O_2 \xrightarrow{CAT} H_2O + O_2$

c. $4H_2O_2 + \text{Guaiacol} \xrightarrow{GPX} 8H_2O + \text{Tetraguaiacol}$

d. $\text{Ascorbate} + H_2O_2 \xrightarrow{APX} \text{Mono-dehydroascorbate} + 2H_2O$

e. $H_2O_2 + \text{Glutathione} \xrightarrow{GR} H_2O + \text{oxidized glutathione}$

The knowledge of morphological and physiological strategies under drought stress has been extensively explored to develop number of transgenic crops with enhanced drought tolerance in previous.

During drought, the occurrence of the osmotic stress usually takes place which is associated with the abscisic acid (ABA) accumulation in the stressed plant. The increased amount of ABA decreases the stomatal conductance to minimize the water loss *via* transpiration (36). Therefore, to cope up with such challenges to agricultural system, the understanding of the effects of drought on plants is very crucial and very important. The water deficit may induce or repress the expression of number of genes. A number of techniques are available for knowing the insights of expression of different genes during stress. The microarray technology, RNA sequencing, transcriptome study etc. are few of them. The recently identified dehydration-inducible genes through microarray technology are mainly divided into two groups:

1. There are some common protein and enzymes which play an important role in the tolerance towards abiotic stress. These are chaperones, late embryogenesis abundant proteins, RNA binding proteins, enzymes for osmolyte biosynthesis, osmotin, RNA-binding proteins, water channel proteins, proline transporters etc. (37).

2. The proteins like transcription factors (TFs), protein kinases, protein phosphatase, enzymes of phospholipids metabolism etc. are the main regulatory proteins (37).

Number of strategies were reported to deal with drought stress and among them ABA engineering is one of the most important. ABA is an isoprenoid (Fig. 3) which act as antitranspirant, inhibitor of fruit ripening and act as growth inhibitor of endodermis of roots under salty environment (38).

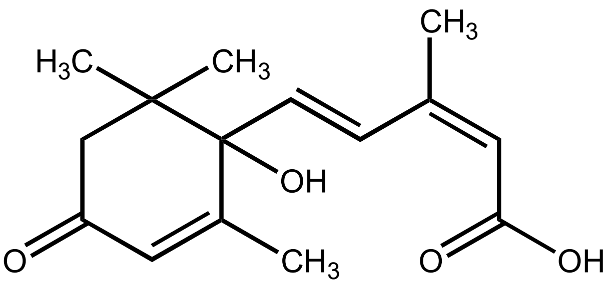

Fig. 3. Structural representation of ABA

ABA biosynthesis take place *via* β-carotene through several enzymatic steps (Fig. 4). Under stressful conditions, number of genes are expressed for biosynthesis of ABA like zeaxanthin oxidase (ZEP), 9-cis-epoxycarotenoid dioxygenase (NCED), ABA-aldehyde oxidase (AAO) and molybdenum cofactor sulphurase (MCSU) (39).

The ABA-induced signal transduction is divided into two types: ABA-dependent and ABA-independent pathway.

ABA-dependent gene expression: During stress, there is elevation in the content of ABA and the increased amount of ABA cause binding of itself with receptors for the initiation of signal transduction. There are three main components of ABA dependent signal transduction:

(i) pyrabactin resistance (PYR)/pyrabactin resistance like (PYL)/regulatory components of ABA receptors (RCAR);

(ii) protein phosphatase 2C (PP2C) and

(iii) sucrose non-fermenting (SNF1) related protein kinase 2 (SnPK2).

In signal transduction of ABA, PP2C act as negative regulator, while SnPK2 acts as positive regulator (40, 41). ABA is known to acts as an

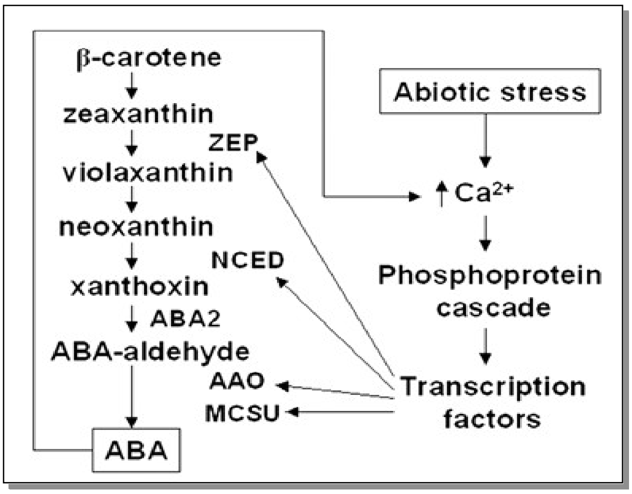

Fig. 4. ABA biosynthesis (39)

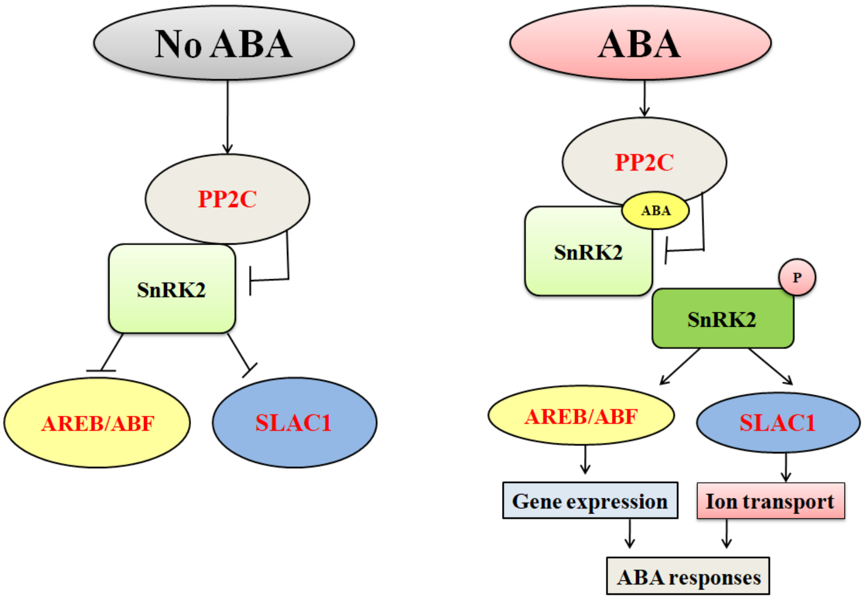

Fig. 5. ABA dependent signaling (52)

endogenous messenger in plants under stressed condition and the promoter regions of many ABA-responsive genes contain a conserved *cis*-element that is ABA-responsive element (ABRE), PyACGTGG/TC which plays major role in ABA-dependent gene expression (37). ABRE also requires another *cis*-acting element which is CE (coupling element) to achieve ABA induction (42). In the absence of ABA or normal conditions, PP2C is bound to SnRK2 which actually ceases the phosphorylation of downstream substrates and no signal transduction takes place. In the presence of ABA, it bound to ABA receptors (RCARs/PYR1/PYL) to form a complex. The formation of this complex provides an active site for the PP2C (negative regulator) and in the presence of ABA, PP2C facilitate the phosphatase activity of SnRK2 which is the first step of ABA-responsive regulation pathway. Thus, multiple step phosphorylation of SnRK2 activates the ABRB (ABRE-binding protein)/ ABF (ABRE-binding factor) which finally induce gene expression (Fig. 5) (43). ARBE and ABF are basic leucine zipper (bZIP) transcription factors (37). Moreover, the activation of these ABA receptors allows SnRK2s to phosphorylate some other target proteins, like S-type slow anion channel (SLAC1) responsible for controlling stomatal response under normal/stressed conditions (44). It is a 10-transmembrane domain protein possesses an extended cytosolic N-terminal region which contains an OST1 phosphorylation site essential for its activity (45, 46). Expression of SLAC1 and OST1 is required for channel activity. SLAC1, itself seldom causes channel activity (29). In ABA-dependent signaling, it was reported that the accumulation of K^+ in guard cell is also SnRK2-dependent. Thus, these receptors, PYR/PYL/RCAR, PP2Cs and SnRK2 play central role in controlling

ABA dependent signaling. Moreover, for terrestrial plants AREB/ABFs is considered more useful and the phosphorylation of AREB/ABF by SnRK2 is also considered as a critical step for enhancing drought tolerance among crops (47, 48, 49, 50). Recently, the evolution of PP2C was reported earlier among terrestrial plants as key regulators of intrinsic desiccation tolerance. The signaling factors such as PYL (*e.g.* PYL4) can also be used for improving stress tolerance among terrestrial plants (51, 52).

ABA-independent pathway: In ABA-dependent pathway ABRE plays main role, while in ABA-independent pathway dehydration responsive element/C-Repea T (DRE/CRT) plays important role and the promoter of this also contains conserved *cis*-acting motif *i.e.* A/GCCGAC (37). The two transcriptional factors CBF/DREB1, CBF/DREB2 (C-repeat binding factor/dehydration-responsive element binding protein) belonging to AP2/ERF family bind to DRE/CRT element (53). It was reported that the interaction of DREB1 with DRE/CRT controls the expression of various stress responsive genes in *Arabidopsis* (54). The drought, salinity and freezing stress-tolerance were recorded to improve during the overexpressing DREB1/CBF TFs in the transgenic *Arabidopsis* but their constitutive expression cause growth defects. Thus, the overexpression of DREB/CBF TFs has been well reported to improve and enhance the drought tolerance in transgenic crops. Therefore, TFs can be used to improve drought tolerance in a variety of crop plants.

Post transcriptional regulation of ABA

The gene expression of ABA can also be controlled after the transcription mainly *via* alternative splicing and RNA silencing (55, 56). The final product of transcription is pre-mRNA which is capped and polyadenylated. During maturation of mRNA, pre-mRNA undergo splicing which is the removal of introns from pre-mRNA. Similarly, alternative splicing (AS) is also removal of introns but it gives rise to more than one mRNA from a single gene. It is mainly of five types: exon skipping, alternative 5' splice site, alternative 3' splice site and intron retention (Fig. 6). According to Reddy et al. (2007) in *Arabidopsis thaliana* 30% transcripts are spliced through AS (57). The splicing is mediated through spliceosome and SERINE/ARGININE RICH (SR) protein is an integral part of that which plays a key role in the regulation of splicing in eukaryotes (58). SR belong to a highly conserved family of RNA-binding proteins and it execute and regulate pre-mRNA splicing in different part of plant in response to stress (59). Alternative splicing results in the availability of different transcripts which ultimately results in the formation of different proteins which might be helpful in drought stress tolerance (55). Moreover, alternative splicing can also auto-regulate the various TFs under stress Guerra et al. (2015) (60). For example, alternative splicing of a transcript encoding DROGHT RESPONSIVE ANKYRIN 1 (DRA1) protein *via* intron retention mechanism is reported to involve in the drought tolerance in *Arabidopsis thaliana* (60).

The RNA silencing is a process of down regulation of some transcripts *via* the action of different small RNAs (56) and in these small-RNAs, the regulations of drought stress were mostly reported *via* micro RNAs (miRNA). These are endogenous small non-coding RNAs which act on target genes of mRNA by sequence pairing thus, inhibiting their translation or cleaving them (61). The various studies reported the role of miRNAs in the development of drought tolerant crops and further should explored.

There are number of transgenic crops have been produced in last decades and some them are Indian mustard, maize, wheat, and rice etc. These were made drought resistant *via* over accumulation of GB, protection of photosynthetic

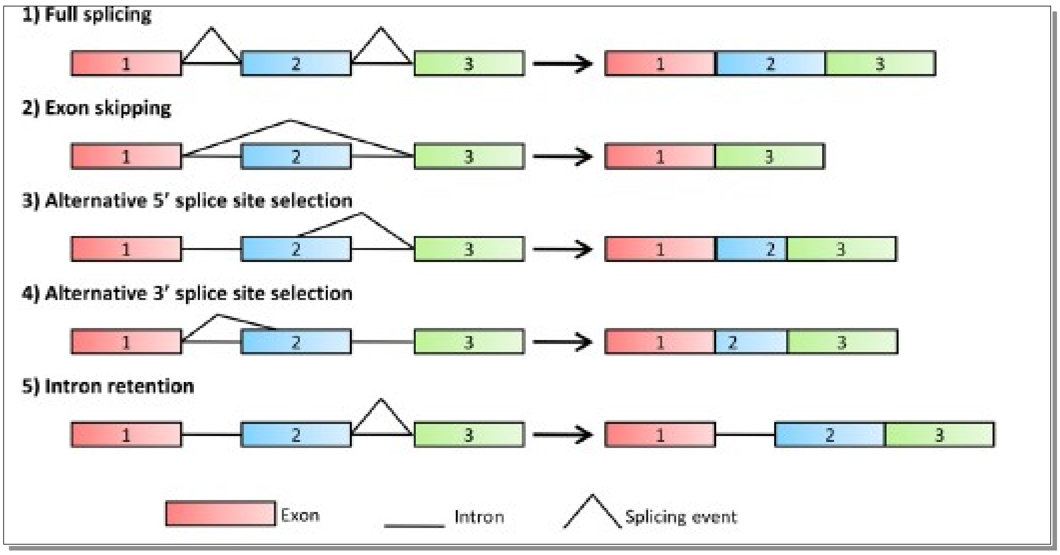

Fig. 6. Types of alternative splicing (60)

machinery from damage caused by dehydration and accumulation of trehalose respectively (62, 63, 64).

Conclusions

The great leaps and bounds in the field of plant drought stress responses and tolerance mechanisms have been achieved in the last decades but many challenges still lie there. Thus, the recent techniques and methods of molecular breeding and advanced biotechnology might be helpful for the development of crops with increased drought tolerance. In this context, relevant genes involve in signal transduction may be useful in enhancing drought tolerance and can further be explored more using different recent technologies. Thus, it can positively influence the capability of the crop plants to deal with the frequent drought stress in such areas which are more prone to drought.

Conflict of Interest

There is no conflict of interest among the authors.

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Authors contributions

All the authors contributed equally to prepare the review article.

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