Journal of Natural Sciences Research
ISSN 2224-3186 (Paper) ISSN 2225-0921 (Online)
Vol.10, No.5, 2020

Review on Role of Absciscic Acid for Adaptation and Performance of Crop Under Drought Condition

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Abstract

There are many biological regulators that enhance crop adaptation and performance under water deficit condition to realize sustainable crop production for food security and ample in put supply for Agro-industry. Hence, the current review conducted with the objectives to understand the effect of ABA for adaptation and performance of crops under drought stress. Absciscic acid (ABA) is one of Plant hormones that principally participate in crop response to drought stress. Its synthesis and catabolism for different function pass through many step in plant cell. After synthesis and catabolism ABA transported to different plant parts for regulatory purpose. ABA plays great role in plant adaptation and performance under drought starting from seedling emergency up to grain yielding by regulating plant cell, organ and organ system reaction to drought; this could be achieved through enhancing seed dormancy (inhibit seed germination during adverse condition) and reduction of water transpiration by promotion of stomata pore closure. Also via facilitating modification in root hydraulic conductivity, photosynthesis, biomass allocation between roots and shoots, plant water relations, osmolyte production, and synthesis of stress-responsive proteins and genes to confer stress tolerance ABA enhance crops performance under severe water deficit.

Keyword: Absciscic acid, Drought tolerance, Gene expression, Stomata closure, Root growth, Shoot growth and Yield performance
DOI: 10.7176/JNSR/10-5-03
Publication date: March 31st 2020

1. INTRODUCTION

Abiotic stresses such as drought is the major threats to agriculture production worldwide starting from vegetative growth up to giving yields (Bray *et al.,* 2000). To provide tolerance against stresses, plants are equipped with several in built physiological and biochemical mechanisms occurring at cellular level. These are plant growth regulators (PGR) like auxins, gibberellins, cytokinins, ethylene and abscisic acid (ABA) (Upreti and Maryada, 2016).

The first target of manipulation of ABA signaling is dehydration tolerance. Stomata regulation and growth rate such as root elongation is also modified by ABA under dehydration (Spollen *et al.,* 2000). In addition to survival under drought, water usage under well-watered conditions can be reduced by enhancement of ABA signaling (Kim and Van Iersel, 2011). Several studies show that over expression of ABA biosynthetic enzymes enhances drought tolerance (Iee *et al*., 2001). These may be mainly caused by lower transpiration rate. The yield of crop plants is also improved by the modification of ABA synthesis. A transgenic rice expressing ABA3/LOS5 is tolerant to drought, resulting in better yields under water deficit condition (Xiao *et al*., 2009).

Thus, mediation of the ABA pathway is a good scheme for the improvement of crops. ABA induces numerous responses in several aspects and the concentration of ABA is important under some conditions. For example, a higher concentration of ABA inhibits seedling growth, while a lower concentration (less than 1 μM) of ABA enhances it (Parcy *et al*., 1994). Since hypersensitivity to ABA confers not only tolerance to dehydration but also inhibition of seed germination and seedling growth; such expression only under stress may be useful.

ABA is important for seed dormancy. While easy and quick germination is good for cultivating, but unexpected germination, such as preharvest sprouting, causes substantial losses in seed yield and quality of cereal crops (Liu *et al.*, 2013). Wheat mutants increasing ABA sensitivity show higher seed dormancy (Schramm *et al.*, 2013). Temporally programmed manipulation or conditional induction of ABA sensitivity may provide controlled germination making significant profits enhancing crops performance under drought condition. Therefore, the objective of this review is to understand the effect of ABA for adaptation and performance of crops under drought stress.

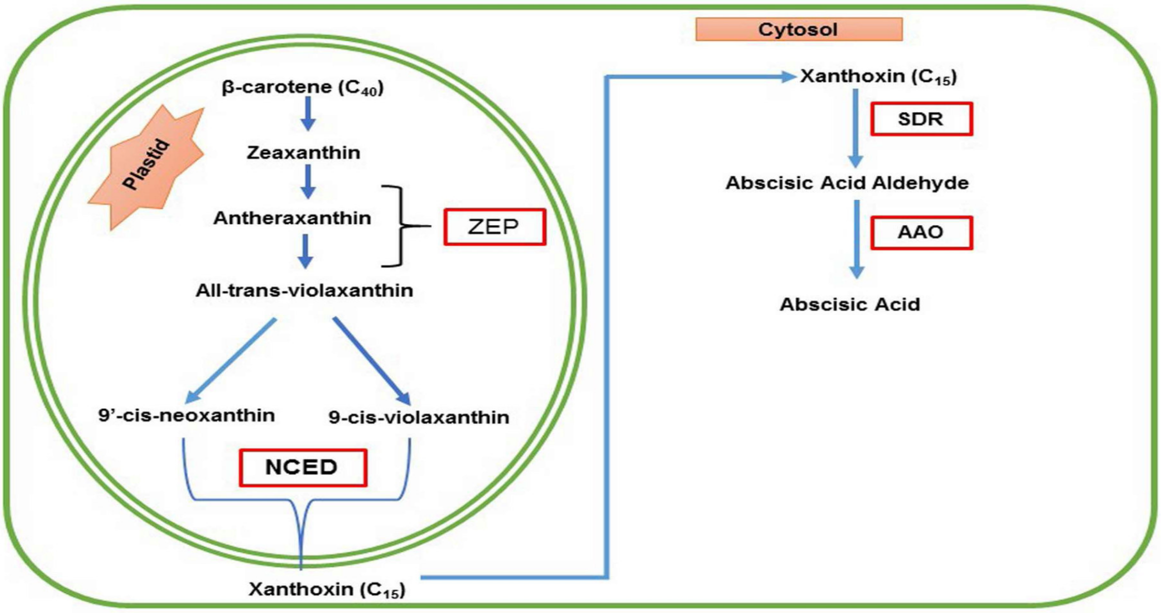
2. LITRETURE REVIEW

2.1. ABA signaling in plants

ABA belongs to the most important phytohormones involved in plant growth, development and adaptation to various stress conditions including water deficit (Verslues *et al.,* 2006). ABA is reported in all kingdoms of life with the exception of Archea (Hauser *et al*., 2011). A dynamic balance of biosynthesis and degradation determines the amount of available cellular ABA which is influenced by developmental and environmental factors such as light, salinity and water stress (Cutler and Krochko, 1999). High cellular ABA levels lead to synthesis of storage proteins in seeds, promote seed desiccation tolerance and dormancy (Finkelstein *et al*., 2008) and inhibit seed germination. ABA is also involved in the control of lateral root formation and seedling growth (Xiong *et al.,* 2006) as well as in the reduction of water transpiration through promotion of stomata pore closure (Kim *et al*., 2010). Moreover, ABA controls the expression of a large set of stress-responsive genes (Nemhauser *et al*., 2006).

2.2. ABA biosynthesis in plant

With the exception of the conversion of xanthoxin to ABA in the cytoplasm, all the steps for the ABA synthesis occur in plastids (Seo and Koshiba, 2002) (Fig.1). The early C5 precursor of ABA, Isopentenyl pyrophosphate (IPP) is produced primarily in plastids via 1-deoxy- D-xylulose-5-phosphate (DXP) from pyruvate and glyceraldehydes- 3-phosphate (Wasilewska *et al.,* 2008). This leads to the sequential production of farnesyl pyrophosphate, geranylgeranyl pyrophosphate (GGPP), phytoene, carotene, lycopene and β-carotene. Β-carotene is converted to a xanthophyll, zeaxanthin, which is the first oxygenated carotenoid (Seo and Koshiba, 2002). Subsequent steps involve the synthesis of cis-isomers of violaxanthin and neoxanthin that are cleaved to form xanthoxin (the C15 precursor of ABA). This cleavage is catalyzed by the 9-cis-epoxycarotenoid dioxygenase (NCED) enzymes (Schwartz *et al*., 2003). Xanthoxin is presumed to migrate from the plastid to the cytosol (Nambara and Marion-Poll, 2005), where it is converted to ABA by three possible pathways: via abscisic aldehyde, xanthoxic acid or abscisic alcohol (Seo and Koshiba, 2002).



Source:-Saroj *et al*., 2016

Figure 1. Schematic representation of biosynthesis of ABA in plants.

ABA is derived from β-carotene (C_{40}) through an oxidative cleavage reaction in plastids. The first step of ABA biosynthesis pathway is the conversion of zeaxanthin and antheraxanthin to all trans-violaxanthin, which will be catalyzed by zeaxanthin epoxidase (ZEP). Antheraxanthin is the intermediate product. All–trans-violaxanthin is converted to 9-cis-violaxanthin or 9 –cis neoxanthin by the 9-cis-epoxy carotenoid dioxygenase (NCED), which yields a C15 intermediate product called xanthoxin. Xanthoxin is then converted into ABA by two enzymatic reactions. Finally, xanthoxin is converted to an ABA aldehyde by the enzyme, short-chain alcohol dehydrogenase/reductase (SDR), and then oxidation of the abscisic aldehyde to ABA is catalyzed by the abscisic aldehyde oxidase (AAO) (Finkelstein and Rock, 2002).

2.3. ABA catabolism for function

Cellular ABA levels can be lowered via two pathways: hydroxylation and conjugation (Nambara and Marion-Poll, 2005). ABA is hydroxylated via oxidation of the methyl groups of the ring structure at three positions, C-7′, C-8′, and C-9′, of which C-8′ is the primary site (Cutler and Krochko, 1999). The three forms of hydroxylated ABA exert significant biological activity (Zhou et al., 2004), but hydroxylation triggers further inactivation steps (Nambara and Marion-Poll, 2005). Cytochrome P450 monooxygenase (CYP707A) catalyzes the hydroxylation of ABA at the C-8′ to form unstable 8′-hydroxy ABA, which is subsequently converted to phaseic acid (PA) by spontaneous isomerization (Saito *et al.,* 2004). PA is then converted to dihydrophaseic acid (DPA) by a soluble PA reductase (Gillard and Walton, 1976).

ABA conjugation apart from de novo biosynthesis, ABA conjugation/ deconjugation plays a critical role in the regulation of cellular ABA amounts under both normal and dehydration conditions (Xu *et al.,* 2012). ABA and hydroxy ABA are conjugated with glucose for inactivation. ABA can be inactivated at the C-1 hydroxyl group by forming different conjugates. Of these conjugates, ABA glucosyl ester (ABA-GE) is the predominant form, which is produced by ABA glycosyl transferase (Cutler and Krochko, 1999). ABA-GE is stored in vacuoles and the apoplast (Dietz *et al*., 2000). The low membrane permeability makes ABA-GE suitable for long distance translocation and storage in vacuoles and the apoplastic space (Jiang and Hartung, 2008). Under dehydration conditions, ABA is released from the glucosyl ester form by β-glucosidases (Xu *et al*., 2012). The enzymatic activity of β-glucosidases to catalyze the hydrolysis of ABA-GE for releasing free ABA was first demonstrated in barley (Dietz *et al*., 2000).

2.4. ABA Transport for regulation purpose in plant cell

Stress-induced biosynthesis of ABA primarily occurs in vascular tissues but ABA exerts its responses in various cells, including distant guard cells (Kuromori *et al*., 2010). Thus, ABA responses require translocation from ABA-producing cells via intercellular transport to allow rapid distribution into neighboring tissues. Recently, cell-to-cell ABA transport was shown to be mediated by two plasma membrane bound ATP-binding cassette (ABC) transporters (Kuromori *et al*., 2010) and a family of low-affinity nitrate transporters (Kanno *et al.,* 2012).Most ABC transporters are integral membrane proteins and act as ATP-driven transporters for a very wide range of substrates, including lipids, drugs, heavy metals, and auxin (Rea, 2007).

2.5. Role of Abscisic Acid in plants performance under drought

The ABA is an important chemical signal of plant responses to a range of abiotic stresses, including drought and salinity (Keskin *et al.,* 2010). A dynamic balance between its biosynthesis and degradation, sensitized by developmental and environmental factors, determines the amount of available ABA (Cutler and Krochko, 1999). The functions of ABA in plants are multiple. High cellular ABA facilitate modifications in stomatal functioning, root hydraulic conductivity, photosynthesis, biomass allocation between roots and shoots, plant water relations, osmolyte production, and synthesis of stress-responsive proteins and genes to confer stress tolerance (Kim *et al.,* 2010).

2.5.1. Seed Dormancy and Germination

Seed is a fundamental organ in higher plants and the transition to seed dormancy and germination signifies a key stage in the plant life cycle, which is an important factor in ecology and economical trait (Saroj, 2016). The ABA plays a central role in the induction and maintenance of seed dormancy. It also inhibits the transition from embryonic to germination growth which is very important during unfavorable condition to save the seedling. During the phase of desiccation tolerance, ABA metabolism must be regulated. For young and mature plant Sometimes, ABA translocates from the roots through xylem or phloem (Miransari and Smith, 2014) to the shoot system to exert its action there.

2.5.2. ABA induce gene expression

ABA signaling leads to large changes in gene expression, which may involve changes in transcription, transcript processing, and stability (Cutler *et al.,* 2010). In Arabidopsis, about 10% of all genes are regulated by ABA (Nemhauser *et al*., 2006). Expression of AREB1/ABF2, AREB2/ABF4, and ABF3/DPBD5 in Arabidopsis regulated by ABA in dehydration and high salinity stresses (Fujita *et al.,* 2005). Over-expression of these factors in transgenic plants resulted in ABA hypersensitivity in germination of seed, growth, and also enhanced drought tolerance (Abdeen *et al*., 2010).

A number of genes that respond to stress at transcriptional level have been found to be induced by ABA (Delasny *et al.,* 1994). However, not all the genes induced by stress are responsive to ABA. There are ABA-dependent and ABA-independent signal transduction cascade between initial signal of stress and expression for specific gene. Gene expressed during stress helps in protecting cells from stress injury by producing proteins involved in signaling transduction mechanism (Shinozaki and Yamaguchi- Shinozaki, 1997).

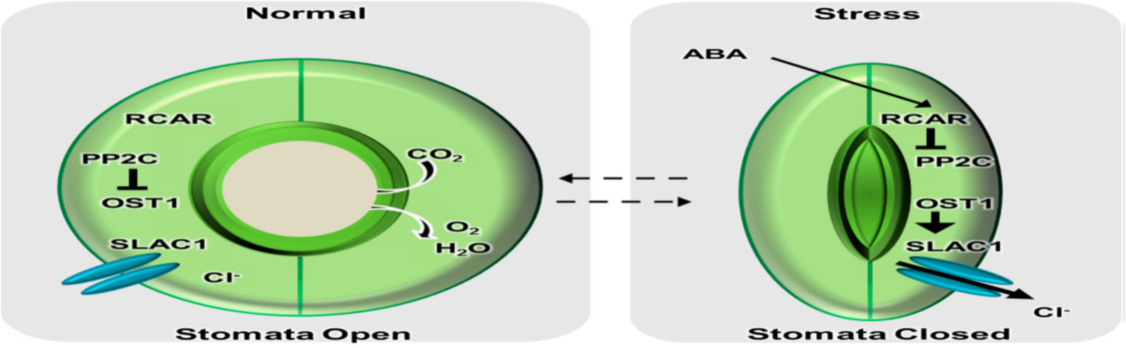
2.5.3. ABA induces stomatal closure

The increases in ABA enable plants to restrict their water loss through transpiration following closure of stomata and enhance plant water status following increase root hydraulic conductivity (Thompson *et al*., 2007). The sensitivity of stomata to ABA varies in plant species and cultivars and is dependent upon leaf age, climatic factors like temperature and relative humidity, plant nutritional status, ionic status of xylem sap, and leaf water status (Dodd *et al*., 1996). Such variations in ABA for stomata response are possibly the consequence of variations in the magnitude of ABA transportation to the active site at guard cell. Tardieu and Simonneau (1998) demonstrated that the xylem ABA concentration and stomata conductance are linearly inverse related and the slope of relationship varied diurnally. Exogenous application of ABA is effective to increase plant adaptive response to various stress conditions (Marcinska *et al.,* 2013).

Light induces stomata ostiole opening, while ABA and elevated CO_2 levels promote closure (Wasilewska *et al.,* 2008) (Figure 2). This aperture regulation is under the control of guard cell turgor. Closing stimuli, including ABA, were shown to inhibit the uptake cellular machinery and trigger ion and water efflux. Elevated cytosolic

Ca^{2+} levels activate two types of anion channels that mediate anion release from guard cells; slow-acting sustained (S-type) or rapid transient (R-type) anion channels (Roelfsema *et al*., 2004). It was proposed that the S-type, and not the R-type, channel is responsible for ABA-mediated stomata closure (Joshi-Saha *et al.,* 2011).

The membrane depolarization caused by anion efflux via ion channels activates outward-rectifying K^+ (K^+ out) channels and results in K^+ efflux from guard cells (Schroeder *et al.,* 2001). The sustained efflux of both anions and K^+ from guard cells drives water efflux and contributes to the loss of guard cell turgor, leading to stomatal closure. ABA also inhibits ion uptake, which is required to initiate hyperpolarization of guard cell plasma membranes to induce stomatal opening.



Source: - Chae *et al.* (2015)

Figure 2. Simplified overview of abscisic acid (ABA) signaling movement via the stomata pathway.

Under normal conditions, 2C-type protein phosphatase (PP2C) family members, which are negative regulators of ABA signaling, suppress open stomata 1 (OST1) kinase activity via physical interaction, leaving the S-type anion channel (SLAC1) with basal activity. Under conditions of stress, including drought, the ABA concentration in leaves increases rapidly (Hubbard *et al*., 2010). ABA perception occurs via regulatory component of ABA receptor (RCAR) family members functioning as ABA receptors in combination with PP2Cs (Cutler *et al*., 2010) (Figure 2). The formation of the RCAR- PP2C complex breaks the PP2C linkage to OST1 complex, there by releasing active OST1 kinase from inhibition. In turn, OST1-mediated phosphorylation induces activation of the SLAC1 channel, then, releasing anions and depolarizing the membrane (Lee *et al*., 2009). This depolarization induces a further drop in turgor and closure of the stomata pores.

2.6. Effects of ABA on root growth

The ABA is also active in root-to-shoot communication in the plants suffered from stress. The ratio between the growth of root and shoot in a plant is sensitive to abiotic stresses, and there is coordination among them via long distance transport of substrates or signal (Munns and Crammer, 1996). Passioura and Stirzaker (1993) reported that the ABA acts as a feed-forward signal from the roots to the aerial plant parts under stress conditions. Jackson (1993) provided evidence for influence of the roots on shoot development via transport of hormones in the xylem. Further Saab *et al.* (1990) stated that the relationship between ABA and root growth is completely different from that in shoots, as higher ABA levels in roots promote root growth at low water potential (Watts *et al.,* 1981). However, some investigations also reported inhibition in root expansion by exogenous applications of ABA (Cramer and Jones, 1996). ABA increase in roots tends to stimulate the water flow by increasing the root hydraulic conductivity and ion uptake, which causes increase in water potential gradient between soil and roots (Glinka and Reinhold, 1971). It also increases water absorbing area of roots and helps the plants transport more water and nutrient under stress situations.

2.7. Effects of ABA on shoot growth

ABA is generally regarded as an inhibitor of shoot growth (Davies, 1995). Initial studies of the effect of decreasing endogenous ABA levels in maize seedlings grown at low water potential (under conditions of near-zero transpiration) were consistent with this expectation (Saab *et al*., 1992). Opposite to this by studying on maize seedlings, Feng (1996) substantiated that the exogenous applications of ABA promotive effect on shoot growth at low water potential appeared to be specific to the water-stressed condition. Feng (1996) verified that a longer duration after transplanting revealed a greater length in the relationship of shoot growth under ABA at low water potential when compared with others like Fluridone (FLU, 10 µM) (Figure 3).

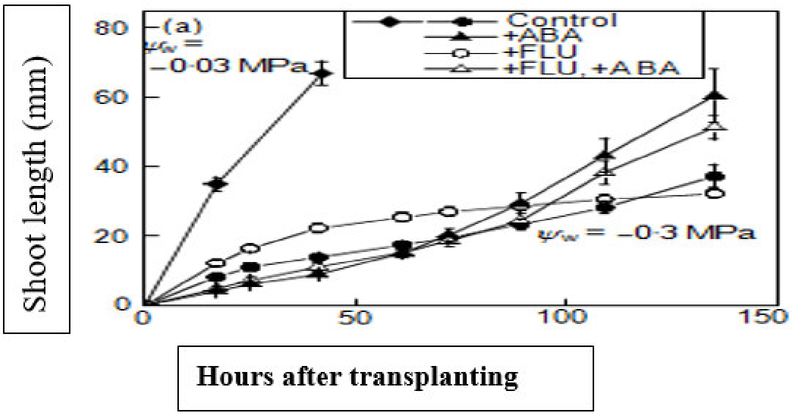


Figure_3. Shoot length increase of maize seedlings (cv. FR27_×_FRMo17) after transplanting to vermiculite at high (-0·03_MPa) and low (-0·3_MPa) water potential (ψ_w). Source: - Feng (1996)

2.8. Effects of ABA on Photosynthesis Efficiency

Successive progress in drought stress of both wheat varieties resulted in a significant decrease in chlorophyll, chl a and b, and a significant increase in carotenoids (car) contents (Hala and Ghada, 2008) (Table1). Under severe water stress, ABA treatment resulted in a significant decrease in photosynthetic pigments contents of sakha 94 plants, whereas insakha 93 there was almost no change. Furthermore, the car/chl a+ b ratio were markedly increased in both wheat varieties with decreasing soil moisture, and spraying the plants with ABA resulted in a decrease in this ratio in sakha 93 and an increase in sakha 94 plants. Rehydration decreased the car/chl a+b ratio particularly in sakha 93. PSII of both wheat varieties decreased under drought stress compared to control well watered plants (Wise, 1995) (Table 1). Spraying the leaves with ABA resulted in a significant increase in PSII activity in severely stressed sakha 93 plants; the opposite trend was recorded for sakha 94 plants. Rewatering significantly increased the PSII activity only in sakha 93; the increase in sakha 94 was insignificant. Hence, ABA improves photosynthesis Efficience of Wheat under drought/water stress.

Table 1. Changes in photosynthetic pigments (mg/g dry mass) and PSII activity (μmol reduced DCPIP/μg chl/mg FM) in the leaves of wheat seedlings (sakha 93 and 94) in response to drought, exogenous ABA and rewatering

ABA Treatment	**WHC%**	**Sakha 93**					**Sakha 94**				
		Chl a	Chl b	Car	Car/chl(a+b)	PSII activity	Chl a	Chl b	Car	Car/chl(a+b)	PSII activity
Control D-ABA	90	35.64a	20.43a	15.54d	0.28	0.417a	34.99a	20.66^{a}	12.39^{f}	0.22	0.430^{a}
	70	34.51a	20.89a	25.88b	0.47	0.340b	28.43a	20.17^{a}	28.32^{e}	0.58	0.307^{b}
	30	24.63c	19.25bc	40.45a	0.92	0.105d	17.84d	15.62^{b}	36.31^{cd}	1.09	0.052^{f}
+50μm ABA	90	36.02a	20.86a	15.92d	0.28	0.420a	33.65a	19.30^{a}	17.94^{f}	0.34	0.307^{b}
	70	31.47b	20.35a	19.74c	0.38	0.364b	26.24b	21.54^{a}	33.11^{cde}	0.69	0.280c
	30	24.89c	18.92bc	26.69b	0.61	0.161c	14.24de	12.66^{bc}	48.23^{ab}	1.79	0.023^{f}
+100μm ABA	90	34.91	22.61a	15.17d	0.27	0.393ab	28.87ab	19.70^{a}	29.91^{de}	0.62	0.168^{d}
	70	30.08b	20.33ab	19.62c	0.39	0.338b	20.64c	20.93^{a}	41.13^{bc}	0.99	0.104^{c}
	30	24.79c	17.02c	27.49b	0.66	0.188c	10.17e	9.68^{c}	52.14^{a}	2.63	0.020^{f}
Control rewatered-ABA	90	36.66a	20.48a	15.41cd	0.27	0.499ab	35.22a	21.65^{a}	13.09^{f}	0.23	0.443^{a}
	70	33.45b	21.69a	14.67d	0.28	0.461c	30.78bc	22.72^{a}	21.08^{d}	0.41	0.392^{b}
	30	23.72d	20.05a	20.22ab	0.46	0.145g	17.66ef	16.65^{c}	26.02^{cd}	0.76	0.061^{f}
Rewatered +50μm ABA	90	35.56a	22.15a	14.88d	0.26	0.507a	34.19ab	19.72^{bc}	14.99^{ef}	0.28	0.392b
	70	31.72bc	20.38a	14.43d	0.28	0.485b	25.88d	21.21^{ab}	31.08^{bc}	0.66	0.328^{c}
	30	25.70d	15.24b	17.75b	0.46	0.258e	14.85fg	12.08^{d}	47.77^{a}	1.77	
Rewatered +100μm ABA	90	34.56ab	22.23a	14.45_	0.25	0.463c	28.09^{cd}	22.55^{a}	21.43^{de}	0.42	0.182^{d}
	70	31.21c	20.14a	15.07d	0.29	0.370d	20.41^{e}	20.24^{ab}	37.82^{b}	0.93	0.118^{e}
	30	24.32d	17.95b	21.11a	0.50	0.228f	10.50^{g}	9.19^{d}	50.11^{a}	2.54	0.062f

LSD, means indexed by the same superscript are not significantly different at $P < 0.05$. Values are the means of 3 independent replicates. Chl, chlorophyll; car, carotenoids; WHC, water holding capacity; 90% WHC, well watered; 70% WHC, mild stress; 30% WHC, severe stress

Source:-Hala and Ghada, 2008

2.9. Effects of ABA on yield performance under drought

Major effect of drought in plant is reduction in photosynthesis, which is due to decrease in leaf expansion, impaired photosynthetic machinery, leaf senescence and finally reduction in assimilates production (Wahid and Rasul, 2005). Drought stress reduced the crop yield due to changes in photosynthetic pigments (Anjum *et al*., 2003) and diminished activities of Calvin cycle enzymes (Monakhova and Chernyadev, 2002). However; the yield of crop improved by the mediation of ABA under drought condition (lee *et al*., 2009) (Table.2). The same result obtained by Xiao *et al.* (2009) transgenic rice expressing ABA3/LOS5 is tolerant to drought, resulting better yield performance under drought condition.

Table 2. Effect of drought stress and abscisic acid (ABA) on spike length (cm), number of grains per spike and 100 grain weight (g) of cv. Punjab-96 and cv. Chakwal-97 subjected to 3 days drought at tillering stage. The ABA (10–6 mol/L) was applied as seed pre sowing for 18 h

Treatments	**Punjab-96**			**Chakwal-97**		
	Length of spike(cm)	Number of grains per spike	100 grain weight(g)	Length of spike(cm)	Number of grains per spike	100 grain weight(g)
Control	7a	35a	6b	8a	31ab	5bc
Drought	5b	24b	5c	7b	26b	5c
Drought + ABA	8a	35a	6ab	8a	39a	6a
ABA	8a	36a	7a	8a	38a	6a

All means which share a common letter in the column are similar otherwise differ significantly at $P < 0.05$, cv.-cultivar

Source:-Bano, 2012

Drought stress caused significant reduction in yield components of cv. Punjab-96 but relatively the yield of cv. Chakwal-97 is affected less (Table 2). The spike length, number of grains per spike and 100 grain weight were significantly decreased under drought stress in cv. Punjab-96. ABA priming completely ameliorated the drought induced inhibition in grain number and 100 grain weight. In cv. Chakwal-97, mild effect of drought stress was observed on the spike length and number of grains per spike. Generally; both varieties show good performance under ABA and ABA with drought when compared with under drought performance which implies that ABA enhancements of crop yield performance under drought stress or its ameliorating effects of drought stress on crop yield reduction.

3. CONCLUSION

Abiotic stresses such as drought become the major threat to agriculture production worldwide.

To overcome such problem plants have several physiological and biochemical mechanisms occurring at cellular level. These are plant growth regulators like hormones. From these hormones Abscisic acid (ABA) is imperative in regulating root and shoots growth and other physiological process during crops subjected to water deficit. ABA follows process like biosynthesis, carboxylation and transportation for its availability and to carry out its function. ABA play great role in regulating plant physiological function to enhance crop adaptability and performance under adverse drought stress environments. It induces stomata closure under drought condition which is useful to inhibit water loss through evaporation. This also enhances plants water use efficiency under drought condition. Exogenous application of ABA also authenticated as it can increase root length and area coverage by root which helps plant to take up water from depth. ABA is important for inducing seed dormancy which inhibit unexpected seed sprout and seed emergence under unfavorable condition. This is crucial to avoid seed quality loss. Regulation of plant physiology and increase in water use efficiency by ABA enables crop to adapt and perform very well under water deficit; hence result better yield under drought stress.

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