



Review

Drought stress in sunflower: Physiological effects and its management through breeding and agronomic alternatives



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ARTICLE INFO

Keywords:

Achene and oil yield

Physiology

Biochemistry

Genetics

Agronomy

Sustainable water management

ABSTRACT

Drought is the most important crop production limiting factor in the changing climate scenario and its intensity is predicted to increase in future. Sunflower is an important oilseed crop having 8% share in the world oilseed production. Although, it is a moderately drought tolerant crop, severe drought causes reduction in the seed and oil production. Therefore, to ensure sustainable sunflower achene and oil production, it is very important to understand the relationship among the physiological, biochemical, genetic and agronomic basis of drought for its sustainable management. Impact of drought stress on various aspects of sunflower has been reported earlier but there is not a single study describing the physiological, biochemical and genetic basis of drought in sunflower at molecular and crop level. In this review manuscript, influence of drought on sunflower achene yield and oil quality has been analyzed critically at both cell, plant and crop level, and the possible management options to mitigate the severity of the drought stress are proposed. Available literature describing the impact of drought stress on physiological and biochemical aspects (like, photosynthesis, water relations, nutrient uptake and oxidative damage), morphological and growth parameters and achene yield and oil quality has been discussed critically. Based on the discussion on the impact of drought stress, various management strategies, such as breeding for drought tolerance (conventional or biotechnological), exogenous application of hormones and osmoprotectants, seed treatment and soil nutrient management has been reviewed and discussed. It is concluded from discussion that sunflower responds to water stress by osmotic adjustments, turgor maintenance, carbon assimilation maintenance and hormonal regulations. A comprehensive research on integration of different management options, including agronomic management, conventional breeding and modern biotechnological advances, is needed for the sustainable improvement of sunflower achene yield and oil quality under drought stress. This may also contribute significantly under a climate change scenario.

1. Introduction

Sunflower (*Helianthus annuus* L.) is an annual oilseed crop globally cultivated on 24.77 million hectares with a production of 44.31 million metric tons and it has 8% share in world oilseed market (USDA, 2016). Sunflower contains 40–50% oil and 17–20% protein, thus have a fair potential to narrow the gap between production and consumption of edible oil and animal feed in the world. Actually, it is a crop of tropical and subtropical regions with semi-arid to arid climate, and frequently

grown in dry lands or on supplementary irrigation. Therefore, the crop is affected by ambient environmental conditions like heat and drought (Pekcan et al., 2015; Robert et al., 2016).

However, in a climate change scenario or/and with the onset of early droughts, the crop may be affected by drought stress (Debaeke et al., 2017). In addition to the hiking problem of water stress, the area devoted to irrigated food production systems is expected to decrease resulting in lesser food production (Alexandratos and Bruinsma, 2012; Farooq et al., 2012). Nonetheless, expansion of irrigated land is not

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possible because of water competition among domestic, industrial and agricultural users (Alexandratos and Bruinsma, 2012). Severe water competition among different users will predominately change the irrigated lands to rain-fed systems and ultimately crops have to suffer from periodic events of drought stress (Elliott et al., 2014). Hence, all of agricultural crops and even the moderately drought tolerant crops such as sunflower will be badly affected by drought stress. Severe drought events have been recorded in Asia and beyond, including the countries with arid and semiarid climates during the last decades (Miyan, 2015; Farooq et al., 2012, 2014), which made management of drought stress more challenging.

Although, sunflower is moderately drought tolerant crop (due to drought escape behavior), it is highly sensitive to drought and heat stresses from early flowering to achene filling due to inefficiency in regulating the leaf expansion and transpiration rates under inadequate availability of soil moisture (García-López et al., 2014). The decline in soil moisture leads to leaf wilting, which results in substantial yield reduction in semi-arid areas receiving the low rainfall (Aboudrare et al., 2006). Several reports indicate that drought stress significantly reduces sunflower achene yield, oil yield and oil quality globally (Soleimanzadeh et al., 2010; Babaeian et al., 2011; Oraki and Aghaalikhana, 2012; Ibrahim et al., 2016). However, the effects of drought stress on sunflower productivity are not same for all the growth stages. Exposure to drought at some specific phenophases like germination, anthesis, and achene filling etc., is the most critical factor causing up to 50% yield reduction in sunflower (Kalarani et al., 2004; Hussain et al., 2008). Early season drought stress suppresses germination, stem elongation and leaf area (Fulda et al., 2011; Fatemi, 2014), while drought stress at anthesis results in the formation of empty achene production due to pollen infertility (Lyakh and Totsky, 2014; Totsky and Lyakh, 2015). More available water at initial growth stages results in good vegetative growth, but the subsequent low moisture availability at flowering and grain filling stages significantly reduces the yield due to high transpiration demands (Aboudrare et al., 2006).

Sophisticated approaches are needed to sustain the productivity of existing crops and meet the challenge of food security in the area of global climate change, increasing population pressure and decreasing resources. Being a rich source of edible oil and protein, sunflower can play a vital role in evading the production gap of edible oil and protein in the world. However, effective use of available germplasm and technology needs to be well explored for sustaining the sunflower productivity under increasing risk of water scarcity. Although many individual efforts have been made to assess the effects of drought stress on sunflower yield and oil quality (Gholamhoseini et al., 2013; Manivannan et al., 2015), determine the role of different management options to mitigate the adverse effects of drought stress, and explore the physiological (Baloğlu et al., 2012; Ghobadi et al., 2013), biochemical and molecular responses (Bowsher et al., 2016) of the crop to drought stress, however, no comprehensive review interlinking all aspects is available.

In this article, effects of drought stress on growth, phenology, light harvesting, assimilate partitioning, nutrient and water relations, achene/oil yield, and oil quality of sunflower have been discussed. Management and crop improvement options for drought tolerance in sunflower are also described.

2. Physiological and biochemical responses to drought stress

The crop plants respond to drought stress through changes in biochemical and physiological cascades that range from photosynthesis to metabolic processes. Plants exhibit various responses at the onset of drought stress, which vary from whole plant to cellular and molecular level. Some major physiological and biochemical responses of sunflower to drought stress are described in the following sections.

2.1. Photosynthesis

Photosynthesis is one of the key metabolic pathways, responsible for growth and development with the help of carbon fixation and light harvesting by plant leaves. Photosynthetic efficiency of plant species depends not only on their genetic potential to absorb light energy and utilize it for the production of carbohydrates, but is also influenced by the environmental stresses (Andrianasolo et al., 2016). It has long been known that instead of being a C₃ plant, sunflower has a high photosynthetic potential (similar to C₄ plant maize) i.e., 25–32 μmol CO₂ fixed m⁻² s⁻¹ of leaf (Fock et al., 1979; Potter and Breen, 1980). The high photosynthetic potential of sunflower is due to the presence of stomata on both sides of the leaf, which results in more tissue permeability for CO₂ diffusion and high RuBisCO activity (Ghobadi et al., 2013; Killi et al., 2017).

The process of photosynthesis in sunflower under drought stress is affected by two distinct mechanisms: (i) through decreased CO₂ diffusion within the leaf due to closure of stomata and (ii) through the inhibition of metabolism of CO₂ (Tezara et al., 1999). Growth and productivity of sunflower is strongly affected under moisture deficit conditions due to low photosynthesis rate resulting due to stomatal closure, thus restricting CO₂ diffusion into the leaves (Flexas et al., 2004). RuBP has a significant role in photosynthesis and is key to dark reaction. The capacity of carboxylation and RuBP regeneration decreases in severely stressed intact leaves (Galmés et al., 2013), but in drought tolerant genotypes its content increases in response to prolonged drought (Pankovic et al., 1999), which indicate more RuBP generation as a sign of drought tolerance.

The stomatal conductance and the assimilation of CO₂ in sunflower leaves reduces with an enhancement in the drought intensity (Correia et al., 2005; Iqbal et al., 2009; Ghobadi et al., 2013); nonetheless a genotypic variability exists for reduction in stomatal conductance and CO₂ assimilation in response to drought stress (Andrianasolo et al., 2016; Iqbal et al., 2009). In a study, Tezara et al. (2002) found an increase in net CO₂ assimilation rate in sunflower seedlings due to elevated CO₂ level with a simultaneous reduction in RuBisCO contents. However, the activity of RuBisCO was enhanced. Thus, we can conclude that the elevated CO₂ increases the efficiency of RuBisCO even under water stress. In a study, Ghobadi et al. (2013) found that drought stress negatively affected the photosynthesis, stay green, photosystem-II photochemical efficiency, and stomatal conductance, and observed variation in genotypic response for aforementioned traits. In another study, Kulundžić et al. (2016) found that the photosynthetic efficiency was decreased in different sunflower genotypes under drought stress. Cechin et al. (2015) also found that drought reduced the stomatal conductance which ultimately reduced the concentration of intercellular CO₂ and photosynthesis.

Drought stress reduces photosynthesis in sunflower through stomatal closure and reduced CO₂ fixation. Stomatal closure mediated restricted CO₂ diffusion in the leaves is more dominating in sunflower compared to CO₂ assimilation. Elevated CO₂ level can compensate the drought induced photosynthetic damage under drought stress.

2.2. Water relations

Sunflower possesses stronger ability to use the available soil water due to strong tap root system. Drought stress affects the sunflower growth and productivity mainly by decreasing the water potential, cell division/expansion, owing to loss of turgor, leaf relative water contents as well as the water potential and its components viz., turgor potential (Ψ_t) and osmotic potential (Ψ_o) (Correia et al., 2006; Kiani et al., 2007a).

Drought stress decreases the water potential in sunflower (Ghobadi et al., 2013). For example, various studies have reported a leaf water potential of -0.48 to -1.74 MPa in sunflower under diverse environmental conditions (Prasad et al., 1985; Rachidi et al., 1993), however, it

can drop below -3.0 MPa under drought stress (Wise et al., 1990). In a study, sunflower lines differing in height responded differently to moisture deficits. Dwarf sunflower lines were more tolerant than the taller ones, and maintained the high tissue water status under drought stress resulting in less yield reduction (Angadi and Entz, 2002b).

Various sunflower cultivars exhibit different behavior with respect to plant water relations. For example, under water deficit conditions, the genotype (i.e. R1 genotype) tolerant to drought maintained a high leaf water potential and wilted faster than those of a drought-sensitive genotype (Ouvrard et al., 1996). Similarly, Hussain et al. (2016) also observed that drought significantly decreased the water relations of sunflower hybrids having different ability of drought tolerance. Indeed, drought stress results in an inadequate water transport from xylem which limits the sufficient nutrient supply from phloem (Ruehr et al., 2009). However, sunflower genotypes maintaining the higher water potential under drought stress maintain an adequate supply of water from xylem, which ultimately maintain an adequate nutrient supply from phloem and thus maintain the water potential levels (Hussain et al., 2016) which are supportive to plant growth under drought stress. Likewise, the genotypes maintaining higher water potential extract the water from the deeper layers of soil, which delays the osmotic adjustments (Angadi and Entz, 2002a; Terzi and Kadioglu, 2006).

Water potential is considered as a reliable indicator of plants' response to water stress and genotypes differ for water potential due to differential ability to absorb water from soil and decrease the water loss through stomata, which maintain the turgor pressure (Siddique et al., 2000; Terzi and Kadioglu, 2006; Bayoumi et al., 2008).

In summary, drought stress decreases the water supply to xylem which decreases an adequate nutrient supply to phloem, thus resulting in the lower water potential. However, a huge variability exists among different genotypes for the maintenance of water potential mainly due to the ability of water absorption and root system. However, the adaptive responses of leaf water parameters to drought stress are variable in sunflower genotypes and needs to be investigated at molecular level in future studies.

2.3. Nutrient uptake

Drought stress decreases transpiration rates and impairs active transport and membrane permeability, which collectively result in reduced absorbing power of crop plants (Kramer and Boyer, 1995). Thus, the nutrient transport from root to shoot is restricted due to weak absorbing power of the crop plants under drought stress.

Nitrogen is the most required element by crop plants and constitute several plant components, including amino and nucleic acids. Soil N-mineralization is reduced by drought stress, which ultimately lowers N availability. A decreased transpiration as a consequence of drought stress is the other factor which lowers N transport from roots to the shoots (Tanguilig et al., 1987). The P uptake is hampered under moisture deficit conditions (Pinkerton and Simpson, 1986). The primary reason of reduced P uptake is restricted translocation of P to shoots even under mild drought stress (Resnik, 1970).

Drought significantly reduces the mineral uptake and disturbs nutrient balances as well (Gunes et al., 2008a), however, plant species and genotypes within species vary in their response to water-deficit stress in this regard (Garg, 2003). Drought induced reduction in N and K uptake in two sunflower hybrids have been recently reported by Hussain et al. (2016). The N and K utilization under drought stress at different growth stages is influenced by number of factors, including physiochemical characteristics of the soil, duration and intensity of drought relative to phenology, and the evolutionary history of the organism (Killingbeck, 2004; Silla and Escudero, 2006). The stomatal closure is hampered by lower K supply because of loss of epidermal cell turgidity (Rahbarian et al., 2011) as stomatal closure needs back pressure exerted by fully turgid epidermal pavement cells, whereas the K accumulation is responsible for the required pressure (Roelfsema and Hedrich, 2002;

Habibi, 2013). Canavar and Kaptan (2014) evaluated the uptake of nutrients (P, K, magnesium [Mg], calcium [Ca], iron [Fe], zinc [Zn], copper [Cu], manganese [Mn] and sodium [Na]) in three sunflower hybrids under drought stress and found negative effect of water stress on the uptake, but genotypes differed in their response. Another study (Gunes et al., 2008a) investigated the uptake of P, K, sulfur [S], Ca, Mg, Fe, Cu, Zn, Mn, chloride [Cl], molybdenum [Mo], silicon [Si], Na, vanadium [V], aluminum [Al], strontium [Sr], rubidium [Rb], titanium [Ti], chromium [Cr], nickel [Ni], bromine [Br], and barium [Ba]) in twelve sunflower genotypes under drought stress. Drought stress reduced the uptake of all the aforementioned minerals.

In conclusion, drought stress hampers mineral uptake in sunflower. Reduced mineralization due to low moisture availability and restricted translocation of minerals to shoots because of low transport are the primary mechanisms of reduced mineral uptake. Impaired active transport and membrane permeability are the other restrictions, which lead to imbalanced nutrition in sunflower under drought stress. The imbalances in nutrients ultimately have serious effects on various growth and developmental process.

2.4. Oxidative damage

Reactive oxygen species (ROS) are free radicals of oxygen, which are continuously produced in plants even under normal condition, as they play an important role in cell signaling. However, overproduction of ROS leads towards the oxidative stress. The major ROS in plant system includes singlet oxygen (1O_2), superoxide (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals (OH), among which OH is the most reactive species (Impa et al., 2012) and these are highly toxic to plant physiological and biochemical processes (El-Shabrawi et al., 2010). Drought stress causes an overproduction of different ROS species (Cechin et al., 2015), which may damage most of the cellular components. Drought stress stimulates the ROS production in sunflower (Soleimanzadeh, 2012) and the superoxide radicals are the most dominant ROS produced in sunflower. Water deficit leads to shrinkage in cell volume, which makes the cellular contents more viscous, ultimately resulting in denaturation and aggregation of proteins (Hoekstra et al., 2001). This phenomenon results in abnormal functioning of enzymes involved in photosynthesis. The partial stomatal closure in response to water deficit limits CO_2 entry and its availability for photosynthesis. This limitation results in reduced carboxylation efficiency of RuBisCO, which increases oxygenation, thus increasing the photo-respiratory losses and ROS production (Noctor et al., 2002). Furthermore, reduced CO_2 fixation of photosynthesis decrease regeneration of NADP⁺, which is final electron acceptor of electron transport chain in chloroplast. Hence over reduction of electron transport chain, results in leakage of electron to O_2 and subsequent production of ROS (Smirnov, 1993; Sgherri et al., 1996). In a study, drought stress enhanced the production of ROS (especially H_2O_2) and leaf malonaldehyde (MDA) contents in sunflower with a simultaneous reduction in the activity of catalase (Gunes et al., 2008a).

It is concluded that drought stress leads to production of ROS in sunflower which react with proteins, lipids and DNA resulting in an ineffective antioxidant enzyme defense system.

3. Morphological, physiological and yield responses

In order to manage the drought stress at morphological and/or physiological level, it is necessary to understand its effects on morphology and physiology of crop plants. Sunflower is moderately drought tolerant crop due to its long and deep root system (Hussain et al., 2013a), which enables it to extract water from deeper soil layers. However, if drought stress prolongs, it poses significant negative effect to sunflower from early stand establishment to maturity and ultimately on yield and oil characteristics (Andrianasolo et al., 2014; Flagella et al., 2002). The effects of drought stress on different growth stages,

and morphological and physiological traits of sunflower are discussed in the following sections.

3.1. Germination and early stand establishment

Germination is the most critical phase in the ontogeny of crop plants. The first effect of early season drought is impaired and erratic germination causing poor crop stand (Farooq et al., 2012). Seed germination is a complex process affected by a number of factors where moisture availability is the most critical (Luan et al., 2014). Drought delays the germination onset (El-Midaoui et al., 2001) with substantial decrease in the actual germination in sunflower (Sajjan et al., 1999). Ample soil moisture is required to initiate the germination process. Imbibition by seeds is the first step, which depends on the water potential gradient between seed and soil. Any decrease in soil water potential causes linear decline in seed germination (Wen, 2015).

Sunflower crop is frequently sown on beds and ridges with poor moisture conditions, and lack of rainfall at this stage may result in erratic germination and seedling emergence (Angadi and Entz, 2002b; Mwale et al., 2003; Kaya et al., 2006) in arid climates where supplementary irrigation is not available. Several studies have reported that drought stress in sunflower negatively influenced seed germination of sunflower (Sajjan et al., 1999; Smok et al., 1993; El-Midaoui et al., 2001) which was indicated through an increase in mean germination time owing to drought stress.

In summary, seed imbibition is the first step in the germination process, however, the soil moisture deficit at this stage restricts the seed to uptake required amount of moisture resulting in poor, erratic and non-uniform seed germination and crop stand.

3.2. Plant growth and development

Drought stress is multidimensional in nature and affects plants at every organizational level. Plant growth is an important phenomenon that is regulated by several morphological and physiological factors. Drought stress after germination has systematic effect on growth with reduction of water potential, relative water contents (Ünyayar et al., 2004) and turgor of plant cells (Benlloch-González et al., 2015), which elevate the concentration of solutes in cytosol. These changes decrease cell elongation, thus leading to growth inhibition (Lisar et al., 2012). Growth inhibition is followed by less carbon assimilation, imbalanced mineral nutrition and accumulation of abscisic acid (ABA), which cause wilting of plants (Farooq et al., 2012; Lisar et al., 2012). The negative effects of drought stress on mineral nutrition and metabolism result in reduction of leaf area and disruption of assimilate partitioning. Considerable reduction in leaf area and associated morphological and physiological traits in sunflower lines under drought stress has been reported which varied with different cultivars (Fernández-Moroni et al., 2012; Lisar et al., 2012).

Drought stress hampers numerous growth and development traits such as root volume (RV), total root length (TRL), stem dry weight (SDW), total dry matter (TDM), chlorophyll contents, plant height, stem diameter, leaf dry weight, leaf area index (LAI), crop growth rate (CGR), net assimilation rate (NAR) and carotenoids (Table 1). It has long been known that drought stress impedes morphological traits like plant height, stem diameter, number of leaves etc. in sunflower (Pirjol-Sovulescu et al., 1974; Sadras et al., 1993; Hussain et al., 2010). Drought stress at vegetative stage reduces main stem height, stem diameter, number of nodes or leaves per plant and leaf area (Turhan and Baser, 2004); whereas an increase in root length at the expense of above-ground dry matter occurs resulting in higher root-to-shoot ratio (Javaid et al., 2015). Drought stress results in reduced leaf area, yellowing and falling of leaves (Göksoy et al., 2004; Nezami et al., 2008) and ultimately small plant canopy area which reduces the radiation use efficiency and photosynthetic activities resulting in low achene yield (Germ et al., 2005; Ghobadi et al., 2013).

Table 1
Effect of drought stress imposed at different growth stages on growth and development of sunflower.

Drought Stress level	Growth Stage	Growth and development trait affected	% Decrease over control	Reference	
Mild Drought	3rd leaf stage	Leaf area index	31.35	Gholamhoseini et al. (2013) Hossain et al. (2010)	
	Whole season	Crop growth rate	9.66		
	Whole season	Net assimilation rate	4.50		
	Whole season	Root volume	4.63	Hemmati and Soleymani (2014)	
	Whole season	Tap root length	5.97		
	Whole season	Leaf dry weight	30.76		
	Whole season	Stem dry weight	20.75		
	Whole season	Total dry matter	11.70		
	Whole season	Leaf area index	16.66		
	Whole season	Chlorophyll	9.68	Oraki and Aghaalikhana (2012)	
	Moderate Drought	Vegetative	Plant height	11.82	Buriro et al. (2015)
		Vegetative	Stem growth	11.62	
		Squaring	Plant height	16.12	Mobasser and Tavassoli (2013)
		Flowering	Plant height	6.45	
		Grain Filling	Plant height	5.64	Eslami (2015)
Pollination		Dry weight	50		
Grain Filling		Dry weight	50		
Whole season		Plant height	6.25	Elsheikh et al. (2015)	
Budding		Plant height	13.13	Farzad et al. (2013)	
Budding		Stem diameter	10.49		
Whole season	Crop growth rate	18.25	Hossain et al. (2010)		
Severe Drought	Whole season	Net assimilation rate	7.20	Canavar et al. (2014)	
	Whole season	Root volume	11.73		
	Whole season	Tap root length	17.02		
	Whole season	Leaf dry weight	38.70	Hemmati and Soleymani (2014)	
	Whole season	Stem dry weight	49.41		
	Whole season	Total dry weight	46.97		
	Whole season	Leaf dry weight	52.48		
	Whole season	Stem dry weight	38.67		
	Whole season	Total dry matter	27.93		
	Whole season	Leaf area index	31.81	Ghobadi et al. (2013)	
	Whole season	Chlorophyll a	15.2		
	Whole season	Chlorophyll b	18.3		
	Whole season	Carotenoid	44.6	Gholinezhad et al. (2009)	
	Whole season	Leaf area index	50.4		
	Budding	Plant height	25.60	Buriro et al. (2015)	
Budding	Stem growth	23.25			
3rd leaf stage	Leaf area index	48.30	Gholamhoseini et al. (2013)		
Whole season	Crop growth rate	37.31	Hossain et al. (2010)		
Whole season	Net assimilation rate	7.20	Hemmati and Soleymani (2014)		
Whole season	Root volume	31.60			
Whole season	Tap root length	36.54			
Whole season	Leaf dry weight	65.61			
Whole season	Stem dry weight	44.65			
Whole season	Total dry matter	45.54			
Whole season	Leaf area index	62.12	Oraki and Aghaalikhana (2012)		
Whole season	Chlorophyll	14.86			
Whole season	Chlorophyll a	24.4	Ghobadi et al. (2013)		
Whole season	Chlorophyll b	25.1			
Whole season	Carotenoid	60.3	Gholinezhad et al. (2009)		
Whole season	Leaf area index	68			
Reproductive	Plant height	30.64	Buriro et al. (2015)		
Reproductive	Stem growth	35.77			
Whole season	Plant height	21.25	Elsheikh et al. (2015)		
Flowering	Plant height	11.11	Farzad et al. (2013)		
Flowering	Stem diameter	13.82			

A common adverse effect of drought stress on crop plants is reduction in fresh and dry biomass production due to decreased leaf area followed by less production of photosynthates (Farooq et al., 2012; Lisar et al., 2012). Reduction in biomass production under drought stress had been observed in numerous studies conducted on sunflower (Tahir and Mehdi, 2001; Fatemi, 2014; Cechin et al., 2015). Santonoceto et al. (2002) studied the accumulation dynamics of dry matter, oil and major fatty acids in different genotypes of sunflower under water stress (100, 67, 33 and 0% deficit water of evapotranspiration) and reported less evapotranspiration by closure of stomata, reduced carbon assimilation, pollen infertility, and decrease biomass production due to water stress. Even with supplementary irrigation, crop can face water stress and responds with low biomass production if irrigation is missed at critical growth stages of the crop. Buriro et al. (2015) and Alahdadi and Oraki (2011) reported that skipping irrigation either at flowering or grain filling proved most lethal for the crop yield and biomass production.

In another experiment conducted by Vijay (2004) to identify the most sensitive growth stage of sunflower to limited water supply, flowering stage was observed as the most critical yield affecting stage. In two other studies, Göksoy et al. (2004) and Demir et al. (2006) reported that sunflower should be irrigated at least three times with full or limited irrigation i.e. at heading, flowering and milking to obtain the highest achene and oil yields. They also suggested that in case of limited water availability, irrigation must not be skipped at flowering. Different levels of drought stress i.e., mild, moderate and severe drought stress results in reduced growth and developmental traits, depending upon the growth stage where the drought stress happens. Mild and severe drought stress, imposed either at vegetative, reproductive stage or whole season reduced total root length to 5.97 and 36.54%, respectively (Table 1). Similarly, total dry matter was reduced to 11.70, 65.61 and 45.54% in response to mild, moderate and severe drought stress imposed at different growth stages of sunflower (Table 1). It is evident that all the intensities of drought stress significantly reduce the growth and development of sunflower compared to well-watered conditions.

In conclusion, drought stress affects all the growth and developmental traits of different sunflower cultivars. Drought stress results in reduced leaf area, yellowing and falling of leaves and ultimately the small plant canopy area, which reduces the radiation use efficiency and photosynthetic activities. These processes result in weaker plant growth and development under water stress.

3.3. Achene yield

Crop yield is a complex trait, which is influenced by genotype, environmental factors and management practices. Sunflower achene yield is significantly reduced by drought stress faced by the plants either at vegetative or reproductive (flowering and milking) growth stages (Göksoy et al., 2004; García-López et al., 2014; Hussain et al., 2015). The intensity of yield reduction in response to drought stress depends on growth stage of the crop, severity of the drought and the drought tolerance ability of genotypes.

Flower initiation and anthesis are important growth phases, which determine the achene yield since higher number of fertile flowers and florets result in higher achene yield (Göksoy et al., 2004; García-López et al., 2014; Hussain et al., 2015). Drought stress at this stage is critical as it is coupled with high temperature, which leads to pollen infertility, low head diameter and reduced yield (Behrouzfar et al., 2007; Göksoy et al., 2004; Elsheikh et al., 2015; Benlloch-González et al., 2015).

Different yield components such as head diameter, capitulum diameter, number of achenes per capitulum, achene weight per capitulum, and 1000-achene are significantly hampered by drought stress (Table 2). Khan et al. (2000) concluded that yield and yield components showed decreasing trend with increasing severity of drought stress (irrigation reduced from 100 to 25% of field capacity). They further concluded that achene yield reduced with increasing drought stress due

to reduction in head diameter, numbers of achenes per head and 1000-achene weight. Significant reduction in growth, and grain yield of sunflower have also been reported with increasing intensity of drought stress (Oad et al., 2002; Kakar and Soomro, 2001).

Although limited water availability during early developmental stages of sunflower severely reduced the achene yield; drought at reproductive stages is the most devastating (Reddy et al., 1998; Reddy et al., 2003; Göksoy et al., 2004; Vijay, 2004; Hussain et al., 2008; Nazarli et al., 2010; García-López et al., 2014). Jabari et al. (2007) reported 83% reduction in seed yield of sunflower under drought stress at flowering due to reduction in number of achene per head and 1000-achene weight. Hussain et al. (2009a,b) reported that drought stress either at budding or flowering stage had negative effects on achene yield. Drought stress at flowering stage causes pollen sterility resulting in less number of achenes per head with lighter weight, which severely reduce achene yield (Unger, 1990; Hussain et al., 2008).

Yield reduction in sunflower has been reported with different extent under drought stress imposed either at vegetative or reproductive stages with mild and/or severe intensities of imposed drought (Table 3). It is depicted from the table that the achene yield is reduced depending upon the severity of drought stress and the critical crop growth stage at which it occur.

It is concluded that drought stress at different growth stages hampers yield components, which ultimately lead towards lower achene yield in sunflower. The yield reduction is the result of disturbed physiological and morphological attributes which ultimately affects the yield contributing traits of the sunflower resulting in lower achene yield under drought stress.

3.4. Oil yield and quality

Sunflower oil is considered high quality edible oil due to low content of palmitic and stearic acid and saturated fatty acids with elevated concentration (up to 90%) of unsaturated fatty acids predominately linoleic acid (Rodríguez et al., 2002). The oil with more density of unsaturated fatty acids (e.g. linoleic acid) is essential as human body cannot synthesize these fatty acids (Eslami, 2015). Hence, the sunflower oil is as a better quality edible oil due to its fatty acid composition (Flagella et al., 2002). Thus, releasing the genotypes with much higher concentration of oleic acid rather than linoleic acid is the major objective of breeding programs.

Drought, either at vegetative or reproductive stages causes a significant reduction in oil yield and quality of sunflower (Flagella et al., 2002; Hussain et al., 2008; Ali et al., 2009) because of reduction in oil contents and achene yield. Fatty acids composition in sunflower is altered by drought stress, particularly the amounts of oleic and linoleic acids are changed under drought stress at different growth stages (Baldini et al., 2002) which change the oxidative properties (Flagella et al., 2002).

Drought stress alters the fatty acid composition, mainly oleic/linoleic acid ratio of sunflower oil known as unsaturation ratio. Similarly the changes in linoleic acid are also caused by enzymatic processes governed by genes coding for oleoyl Δ -9 desaturase and oleoyl Δ -12 desaturase, which are main enzymes utilized in metabolic processes related to oleic and linoleic acids, respectively (Cantisani et al., 2000; Rondanini et al., 2003; Lacombe et al., 2004). The up and down regulation of these genes under drought stress alters the oil composition of sunflower (Anastasi et al., 2010). On the other hand, drought stress accelerates earlier embryo development and stimulates enzymatic activities of fatty acid biosynthesis, including oleoyl Δ -12 desaturase, which alters the composition of sunflower oil (Baldini et al., 2002).

The variation in oleic acid is highly dependent on the synthesis or activation of oleate desaturase enzyme, which is affected by water supply (Roche et al., 2006; Baldini et al., 2002). The activity of the enzyme is also affected by disturbed mineral nutrition under drought stress. Different genes govern the variation in unsaturated fatty acids in

Table 2
Effect of drought stress imposed at different growth stages on yield components of sunflower.

Drought Stress level	Growth Stage	Yield component affected	% Decrease over control	Reference
Mild Drought	Budding	Capitulum diameter	19.64	Farzad et al. (2013)
	Whole season		+5.88	Elsheikh et al. (2015)
	Vegetative		4.69	Buriro et al. (2015)
	Whole season		27.97	Alahdadi and Oraki (2011)
	Whole season	Number of achenes per capitulum	12.46	Hemmati and Soleymani (2014)
	Vegetative		3.03	Buriro et al. (2015)
	Whole season		35.47	Alahdadi and Oraki (2011)
	Whole season		14.00	Nezami et al. (2008)
	Whole season	Achene weight per capitulum	25.00	Nezami et al. (2008)
	Whole season	Number of filled seeds	7.62	Elsheikh et al. (2015)
	Budding	1000-achene weight	16.01	Farzad et al. (2013)
	Whole season		5.88	Elsheikh et al. (2015)
	Squaring		19.73	Mobasser and Tavassoli (2013)
	Flowering		27.45	
	Grain Filling		14.58	
	Whole season			
	Vegetative		3.20	Buriro et al. (2015)
	Whole season		36.36	Alahdadi and Oraki (2011)
	Whole season		14.63	Nezami et al. (2008)
	Moderate Drought	Budding	Capitulum diameter	12.49
Whole season		Number of achenes per capitulum	29.79	Hemmati and Soleymani (2014)
Budding			28.80	Buriro et al. (2015)
Whole season			29.05	Gholinezhad et al. (2009)
Budding		1000-achene weight	14.95	Buriro et al. (2015)
Whole season			13.15	Gholinezhad et al. (2009)
Whole season		Grain weight per plant	38.00	Gholinezhad et al. (2009)
Flowering		Capitulum diameter	22.51	Farzad et al. (2013)
Severe Drought	Whole season		11.76	Elsheikh et al. (2015)
	Reproductive		20.18	Buriro et al. (2015)
	Whole season		42.65	Alahdadi and Oraki (2011)
	Vegetative		18.78	Hussain et al. (2016)
	Whole season	Number of achenes per capitulum	45.27	Hemmati and Soleymani (2014)
	Reproductive		44.32	Buriro et al. (2015)
	Whole season		44.67	Gholinezhad et al. (2009)
	Whole season		53.31	Alahdadi and Oraki (2011)
	Whole season		48.33	Nezami et al. (2008)
	Whole season		27.48	Flagella et al. (2002)
	Whole season	Achene weight per capitulum	83.33	Nezami et al. (2008)
	Whole season	Number of filled seeds	21.35	Elsheikh et al. (2015)
	Whole season	1000-achene weight	9.80	Elsheikh et al. (2015)
	Flowering		27.14	Farzad et al. (2013)
	Whole season			
	Whole season		21.80	Gholinezhad et al. (2009)
	Whole season		47.90	Alahdadi and Oraki (2011)
	Reproductive		23.92	Buriro et al. (2015)
	Whole season		31.70	Nezami et al. (2008)
	Whole season		23.69	Flagella et al. (2002)
Whole season	Grain weight per plant	54.49	Gholinezhad et al. (2009)	

standard and oleic sunflower genotypes, which are differentially affected by ambient environmental conditions (Lacombe and Bervillé, 2001; Martínez-Rivas et al., 2001; Pérez-Vich et al., 2002; Schuppert et al., 2006).

The oil of sunflower cultivars grown for edible oil contains four essential fatty acids viz. palmitic, stearic, oleic and linoleic acids (Monotti, 2003). However, no effect of drought stress on oil quality and contents was noted in some studies (e.g. Petcu et al., 2001), which may be due to low intensity of stress and use of high oleic sunflower genotypes. Limited water supply from flowering to physiological maturity increases the oleic acid and decreases the linoleic acid contents compared with well-watered plants as described above (Flagella et al., 2000). Drought stress decreases achene oil contents at the expense of protein contents (Reddy et al., 2003; Daneshian et al., 2005). In most of the cases oil yield reduction is less than seed yield reduction which indicates increase in oil contents. But severe drought at flowering and bud stage reduced oil yield more than seed yield which may be due to decrease in seed oil contents (Tables 3 and 4). So these two stages may be regarded as the most sensitive to drought stress.

Sunflower oil yield and quality are severely hampered by drought

stress, mainly due to reduced activity of enzyme oleate desaturase. However there are some reports where drought stress had no effect on the oil quality of sunflower, which might be attributed to genetic potential of the genotypes used in the studies. More studies are needed to check the influence of drought stress and its intensity on the oil yield and oil quality of diverse sunflower genotypes under an array of climatic conditions across the globe.

4. Management strategies

In theory of evolution by Darwin, he describes “survival of the fittest” which means that fit individual survived and other diminished. Only those crops are successful under harsh environment which can withstand stress. It is crucial for crop scientist to develop strategies which can make the crop plants fit for harsh environmental conditions under climate change scenario. Various management strategies have been opted by different scientist in different agro-climatic regions to improve the sunflower performance under drought stress. These strategies are discussed critically in the following section.

Table 3
Sunflower seed yield and oil yield reduction under drought stress.

Drought stress level	Growth stage	Decrease in seed yield over control (%)	Oil yield reduction	Reference	
Mild drought	Budding stage	10.2	19.3	Hussain et al. (2008)	
	Whole season	51.83	5.61	Alahdadi and Oraki (2011)	
	Whole season	41.89	NA	Gholinezhad et al. (2009)	
	Vegetative stage	15	NA	Heidari and Karami (2014)	
	Vegetative stage	NA	9.70, (8.43)	Ali et al. (2009)	
	Reproductive stage	NA	7.61, (7.30)	Ali et al. (2009)	
	3rd leaf stage	37.5	4.3	Gholamhoseini et al. (2013)	
	Whole season	11.69	NA	Hossain et al. (2010)	
	Vegetative stage	7.63	NA	Buriro et al. (2015)	
	Whole season	17.38	+ 3.08	Mobasser and Tavassoli (2013)	
	Squaring	31.06	38.86, (7.93)	Mobasser and Tavassoli (2013)	
	Flowering	30.63	39.39, (11.93)	Mobasser and Tavassoli (2013)	
	Grain Filling	12.34	22.22, (9.40)	Mobasser and Tavassoli (2013)	
	Pollination	NA	6.93, (+ 6.25)	Eslami (2015)	
	Grain Filling	NA	15.91, (+ 12.5)	Eslami (2015)	
	Whole season	20.80	21.14, (0.43)	Hemmati and Soleymani (2014)	
	Whole season	6–13	NA	Elsheikh et al. (2015)	
	Flowering	34.05	NA	Farzad et al. (2013)	
	Moderate drought	Whole season	25	NA	Gholinezhad et al. (2015)
		Whole season	21.86	NA	Hossain et al. (2010)
Budding stage		33.09	NA	Buriro et al. (2015)	
Whole season		48.44	48.99, (1.03)	Hemmati and Soleymani (2014)	
Whole season		42.31	43.50	Gholinezhad et al. (2012)	
Severe drought	3rd leaf stage	50	11.5	Gholamhoseini et al. (2013)	
	Vegetative stage	37	5.8	Iqbal et al. (2005)	
	Reproductive stage	24	5.6	Iqbal et al. (2005)	
	Vegetative stage	44	NA	Gholinezhad et al. (2009)	
	Vegetative stage	61	NA	Iqbal et al. (2009)	
	Reproductive stage	40	NA	Iqbal et al. (2009)	
	Vegetative stage	15.90	19.3	Hussain et al. (2008)	
	Flowering stage	24.2	29.9	Hussain et al. (2008)	
	Whole season	213.03	20.99	Alahdadi and Oraki (2011)	
	Whole season	57.86	NA	Gholinezhad et al. (2009)	
	Whole season	49	NA	Gholinezhad et al. (2015)	
	Whole season	51.71	NA	Hossain et al. (2010)	
	Reproductive stage	56.36	NA	Buriro et al. (2015)	
	Whole season	66.85	66.88, (0.10)	Hemmati and Soleymani (2014)	
	Whole season	59.04	61.26	Gholinezhad et al. (2012)	
	Whole season	43–48	NA	Elsheikh et al. (2015)	
	Grain Filling	46.83	NA	Farzad et al. (2013)	

The + sign indicates an increase rather than decrease. The figures in parenthesis in oil yield column represent oil percentage. NA denotes that the respective trait was not assessed in the study.

4.1. Breeding approaches

4.1.1. Screening of drought tolerant germplasm and development of tolerant variety through breeding

Exploration of genetic variation is the primary step towards improvement of drought resistance of crops. Such variation exists in wild types and modified genotypes that have evolved under natural selection and considered as the finest source of resistance traits. Appraisal of these resources via an integrated phenotyping and genotyping method in field circumstances together with traits identification that are directly related with yield are important for improvements in drought resistance.

Genetic variability must be expanded for developing successful drought tolerant lines as significant variations are present among sunflower cultivars to attain better yield under drought stress (Rauf, 2008). A high degree of genetic variability in water status, osmotic adjustments, root characteristics, gas exchange parameters, seedling establishment and drought susceptibility index was observed within a large number of sunflower genotypes belonging to diverse origins (Table 5). Hence improvements in these traits through selection from the available germplasm could possibly improve the drought tolerance of sunflower.

Selection of leaf area index with net assimilation rate may be preferred over leaf area for selecting genotypes under drought stress (Hemmati and Soleymani, 2014). Root system is another important trait

related to drought stress tolerance. Generally, deeper roots along with higher root-to-shoot ratio is an adaptive mechanism for drought tolerance and can be used in breeding program to develop drought tolerant sunflower genotypes (Gomes et al., 2005; Rauf and Sadaqat, 2008b). Yield associated traits like root length, upper and lower root weight, root diameter and seedling recovery after reliving the stressful environment are used as important criteria for breeding to develop drought tolerant sunflower genotypes (Rauf and Sadaqat, 2008a,b). Numerous other potential traits are reported that could be used for screening of drought stress tolerance which are positively correlated with yield (Table 4). Drought stress index (DSI) is calculated on the basis of a ratio between yield under drought stress to the yield under no stress conditions and is important for drought stress tolerance. Therefore, this trait may also be useful for breeding of sunflower drought tolerant genotypes (Feres et al., 1986; Baldini et al., 1992; Alza and Fernandez-Martinez, 1997; Rauf and Sadaqat, 2007).

Morphological, physiological and biochemical responses of the plant to drought stress demonstrates its tolerance nature (susceptible or tolerant). But analyses of most of these traits is needed to be conducted by growing the crop for full growth season. This not only become a time consuming, but also required a lot of resources and techniques, which are normally not available at all laboratories. To manage this problem, genes responsible for such traits are identified and closely linked markers are developed. With the help of these markers, plants can be identified for stress tolerant traits at early stages of development with

Table 4
Effect of drought stress imposed at different growth stages on oil quality of sunflower.

Drought Stress level	Growth Stage	Oil constituent affected	% Change over control	Reference	
Mild Drought	Pollination	Linoleic acid	15.85	Eslami (2015)	
	Grain Filling	Linoleic acid	– 40.24		
	Pollination	Oleic acid	36.36		
	Grain Filling	Oleic acid	72.72		
	Pollination	Stearic acid	76		
	Severe Drought	Grain Filling	Stearic acid	160	Flagella et al. (2002)
		Pollination	Palmitic acid	23.75	
		Grain Filling	Palmitic acid	– 50	
		Whole season	Palmitic acid	– 7.89	
		Whole season	Stearic acid	10.52	
Severe Drought		Whole season	Oleic acid	3.24	Ali et al. (2009)
		Whole season	Linoleic acid	– 27.18	
		Vegetative	Palmitic acid	6.27 to 39.55	
		Reproductive	Palmitic acid	10.30 to 39.55	
		Vegetative	Stearic acid	5.56 to 9.93	
	Reproductive	Stearic acid	0.31 to 28		
	Vegetative	Oleic acid	4.69, – 7.93		
	Reproductive	Oleic acid	8.83, – 7.93		
	Vegetative	Linoleic acid	6.30		
	Reproductive	Linoleic acid	– 9.94		
	Vegetative	Linolenic acid	– 35.91		
	Reproductive	Linolenic acid	37.19		
	Vegetative	Total saturated fatty acids	– 0.77		
	Reproductive	Total saturated fatty acids	16.41		
	Vegetative	Total unsaturated fatty acids	– 1.44		
	Reproductive	Total unsaturated fatty acids	– 3.44		
	Vegetative	Alpha-tocopherol	8.61		
	Reproductive	Alpha-tocopherol	60.73		
	Vegetative	Delta-tocopherol	0.58		
	Reproductive	Delta-tocopherol	137.89		
Vegetative	Gamma-tocopherol	90.08			
Reproductive	Gamma-tocopherol	352.85			
Vegetative	Total tocopherols	16.76			
Reproductive	Total tocopherols	103.52			

The – sign with numeric in% change over control column indicate a decrease, no sign with numeric indicate an increase and multiple values within a column indicate% change in different genotypes.

very less resources which saves time and money. Furthermore, introgression of traits in succeeding generations has also been verified with same markers. Successful screening of sunflower genotypes for drought stress tolerance has been reported (Adiredjo et al., 2014a; Ghaffari et al., 2013; Sarazin et al., 2017). As most of the morphological and physiological traits associated with drought stress tolerance are negatively correlated, DSI seems the most suitable traits describing the relative overall performance.

Evolution of drought tolerant sunflower varieties/hybrids through breeding programs is highly important to boost up the global sunflower production under water limited environments (Rauf and Sadaqat, 2007). Different studies have used numerous traits such as stomatal conductance, osmotic adjustment, shoot and root length, photosynthetic rate, leaf area index, malondialdehyde contents, seedling traits, harvest index, drought susceptibility index, root system, leaf hydraulics, chlorophyll fluorescence, canopy temperature, stem diameter, and number of achenes per capitulum for selection of drought tolerance in sunflower (Table 5). The use of these traits is reported to improve the drought tolerance of sunflower to significant extent.

4.1.2. Introgression from wild relatives

The genus *Helianthus* has 51 species and 19 subspecies, with 14

Table 5
Potential traits for screening sunflower genotypes for drought tolerance.

Trait	Correlation with yield	Reference
Stomatal conductance	Yes	Rauf and Sadaqat (2008b)
Osmotic adjustment	Yes	Rauf and Sadaqat (2008a)
Shoot and root length	Yes	Manivannan et al. (2007)
Photosynthetic rate	–	Kiani et al. (2007b)
Malondialdehyde contents	–	Soleimanzadeh et al. (2010)
Seedling traits	Yes	Rauf (2008)
Harvest index	Yes	
Drought susceptibility index	–	
Root system	Yes	
Leaf hydraulics	–	
Chlorophyll fluorescence	Yes	Kiani et al. (2008)
Leaf hydraulics	–	Rauf et al. (2009)
Canopy temperature, stem diameter	Yes	Alza and Fernandez-Martinez (1997)
Osmotic adjustment	Yes	Chimenti et al. (2002)
Head diameter, number of achene and chlorophyll content	Yes	Darvishzadeh et al. (2011)

annual and 37 perennial species (Seiler, 2007). Wild species of sunflower may have some genes related to water stress tolerance which can be exploited by specific hybridization. Therefore, induction of drought tolerant genes from the wild relatives in locally planted sunflower varieties/hybrids may help to develop drought tolerant sunflower varieties/hybrids (Mohan and Seetharam, 2005). Sunflower has been ranked 5th out of 13 most important crops surveyed from 1980's to 2005 which could be improved through introgression from wild relatives (Seiler et al., 2017). It is reported that all *Helianthus* species, except *Helianthus agrestis* P., can be used to introgress traits with conventional back cross method. *Helianthus argophyllus* and *Helianthus anomalus* (wild species) have been extensively used by sunflower breeders to introgress drought tolerant traits like, higher water use efficiency, improved drought sensitivity index and a high harvest index under water stress, to the cultivated genotypes (Baldini and Vannozzi, 1998; Baldini et al., 1999; Griveau et al., 1998; Seiler, 2007). Wild species gene introgression also upgrades the fatty acid composition and protein quality and tolerance to nutrient stress (Korrell et al., 1996; Brouillette and Donovan, 2011). Seiler et al. (2010) reported two sunflower cultivars (HA 429 and HA 430) introgressed for salt and water stress tolerance traits from wild relatives. But in some cases introgression of drought tolerant genes from many wild species has also been associated with the degradation of oil yield in cultivated sunflower (Seiler, 2007) which must be rectified through successive back cross breeding.

It is concluded that selection and conventional breeding approaches are feasible tools which can be used for developing drought tolerant sunflower cultivars. However, too few works have been conducted to realize the potential of these approaches. Conventional approaches must be accompanied with molecular techniques to fasten the process of selection and development of genotypes. Furthermore, wild relatives may also be used more extensively to enhance the genetic variability of available germplasm for drought stress tolerance.

4.1.3. Identification of quantitative trait loci (QTLs) for water use efficiency

Water use efficiency is the measure of ability of a crop to convert water into plant biomass. In a study, Canavar et al. (2014) reported that the selection for water use efficiency using the indirect $\Delta^{13}C$ isotope can be a useful tool in sunflower breeding programs aimed at developing the drought tolerant sunflower genotypes. The identification of quantitative trait loci (QTL) controlling the water use efficiency might also be beneficial for improving sunflower performance under drought

stress. For example, Adiredjo et al. (2014a) identified nine QTL controlling the water use efficiency in sunflower under drought stress. Another single QTL for phenotypic response controlling the water use efficiency was also identified. In recent years, use of leaf carbon isotope discrimination has been emerged as an indirect tool for breeding for water-use efficiency in multiple crops. For example, Adiredjo et al. (2014b) studied the genetic variability in four sunflower genotypes for assessing the phenotypic correlations between the leaf carbon isotope discrimination and water use efficiency. They measured water use efficiency at leaf level and whole plant level. They observed significant differences among the four sunflower genotypes for water use efficiency and leaf carbon isotope discrimination at leaf level and whole plant level. There existed a strong negative co-relation between whole plant/leaf level water use efficiency and leaf carbon isotope discrimination with a decrease in water availability. They suggested leaf carbon isotope discrimination as a pertinent and valuable trait to select the sunflower genotypes with high water use efficiency under drought stress (Adiredjo et al., 2014b).

4.2. Biotechnology and functional genomics

Biotechnology and functional genomics of environmental stresses like drought, heat and salinity has a prodigious contribution to a better understanding of plant adaptation to adverse environmental conditions.

Drought tolerance is a multi-genic traits as it is a combination of many traits which make ecological adaptation of a plant to drought stress. Research on functional genomics has provided genetic basis of most of these traits. Gene products involved in the adaptation of plants to drought stress can be classified in to i) directly involved in stress tolerance (includes dehydrins and chaperons that protect cellular structure during stress, enzymes for osmolytes synthesis that regulate cellular and tissue processes and detoxifying enzymes which detoxify the products produced due to stress) or ii) indirectly involved through regulation of others genes (includes transcription factors which regulate the expression of directly involved genes) (Kasuga et al., 1999). Roche et al. (2007) reported differential expression of genes in drought tolerant and sensitive cultivars which might be associated with the expression of mRNA in different environments (Giordani et al., 2011) which is regulated with indirectly involved genes.

Giordani et al. (2011) reported that these changes in the expression of mRNA can only be studied by using genomic DNA of purely homozygous plants. It was further reported the changes in the expression of genes were related to sequences variability in stress responsive genes. The sequence variability is observed more for directly involved genes compared to indirectly involved genes. Therefore, it can be extracted from the discussion that directly involve genes are more likely to be regulated with external harsh environment.

It is therefore concluded that along with DNA markers, these miRNAs and cDNA markers may also be utilized in developing sunflower cultivars exhibiting higher drought tolerance.

4.3. Agronomic approaches

4.3.1. Exogenous application of hormones and osmoprotectants

Exogenous applications of phytohormones and osmoprotectants may help alleviating drought stress in sunflower (Hussain et al., 2008, 2009a,b; Babaeian et al., 2011; Rabert et al., 2014). Exogenous application of different synthetic compounds such as abscisic acid, potassium chloride, foliar or root application of salicylic acid and ascorbic acid, calcium chloride, sodium nitroprusside as donor of nitric oxide, triazole compounds and glycinebetaine significantly improved the growth, development, biochemical attributes, yield and yield related traits, including morphological, physiological and biochemical traits (Table 6).

For instance, exogenous application of glycine betaine (GB) and salicylic acid (SA) significantly improved the achene and oil yield of sunflower subjected to drought stress at vegetative and reproductive

phase (Hussain et al., 2008, 2009a,b). Zaidi et al. (2015) reported that foliar application of SA significantly improved the proline, sugars and proteins in drought stressed sunflower indicating that exogenous SA application plays an important role in drought tolerance. Significant improvements in antioxidant enzymes and biochemical traits of drought stressed sunflower have been reported by 28-homobrassinolide application (Filová, 2014). Abscisic acid (ABA) application at budding or flowering helped in mitigating the detrimental effects of drought stress and produced better yields compared to no application treatments (Hussain et al., 2014). ABA application also have been reported to regulate some stress responsive genes and proteins in sunflower under drought stress (Shinozaki and Yamaguchi-Shinozaki, 2007). For instance, HaACCO₂ transcript is accrued in leaves and exogenous ABA application induces this gene in sunflower in response to drought stress (Boursiac et al., 2013).

Nitric oxide (NO), is lipophilic in nature and highly diffusible through cellular membrane and involved in many physiological, biochemical and developmental processes in plants (Krasylenko et al., 2010; Cechin et al., 2015). Cechin et al. (2015) reported that application of 10 μM sodium nitroprusside (SNP) a NO donor, significantly improved the concentration of ROS scavenging enzymes which significantly imparted drought tolerance to sunflower. Partial amelioration of adverse effects of drought stress in sunflower has been observed through the application of triazole compounds such as Hexaconazole, Tebuconazole and Propiconazole (Rabert et al., 2014, 2016) which have been reported to strengthen the antioxidant defense system of sunflower through increased activities of antioxidant enzymes such as SOD, APX and CAT.

It is concluded that exogenous application of osmoprotectants, phytohormones, micro and macro nutrients and several other compounds have been proved effective to improve sunflower growth, yield and oil quality under drought stress. Therefore, proper crop nutrition is an agronomic tool which can be employed to improve drought resistance of sunflower.

4.3.2. Use of mineral nutrients and organic manures

Drought stress hampers the transport of nutrients towards roots, thus affecting the cell division and expansion of roots which might be due to reduced transpiration rate. Limited water supply affects the uptake of essential elements. However, an adequate nutrition of plants under water deficit may improve the performance of crops.

Nitrogen (N) and potassium (K) are primary macronutrients, required by plants in large amounts and govern several developmental processes such as photosynthesis, translocation of photosynthates from roots to shoots, protein synthesis, stomatal closure, water-use efficiency and regulation of enzymes (Salami and Saadat, 2013). The application of these nutrients enhance the tolerance against drought stress by improving protein synthesis, stomatal regulation, homeostasis and osmoregulation through quenching the ROS (Cakmak, 2005). Under drought stress, the role of N role in improving growth and plant water relations is well established (Saneoka et al., 2004). Likewise, improved K nutrition results in improved water uptake, maintains plant turgor and regulates stomatal aperture (Bukhsh et al., 2012). Recently Hussain et al. (2016) has reported that combined application of N and K improves drought resistance of sunflower by improving turgor maintenance, enhanced accumulation of osmoprotectants, increased stomatal conductance and net photosynthesis, reduced production of ROS, ultimately ending with higher yield.

Different potassium (K) levels in soil have considerable role in growth regulation and water uptake ability of sunflower. It is well known fact that K deficiency lowers plant resistance to drought stress (Marschner, 1995) through stomatal closure and thus lowers the transpiration rates (Hsiao and Lauchli, 1986). However, some authors also reported that moderate K starvation may cause anomalous stomatal behavior and has a positive effect on transpiration in some crops like wheat and sunflower (Brag, 1972; Lindhauer, 1985). Fournier et al.

Table 6
Different management interventions in improving drought tolerance of sunflower and traits improved.

Management option	Growth stage	Improved trait	Reference
Biological Seed Priming			
Inoculation with plant growth promoting rhizobacteria	Seed	Relative water contents	Singh et al. (2015)
Inoculation with plant growth promoting endophytic bacteria	Seed	Seedling growth	Forchetti et al. (2010)
arbuscular mycorrhizal inoculation	Seed	Seedling growth	
		Dry matter	Gholamhoseini et al. (2013)
		Seed weight	
		Seed and oil yield	
Exogenous application of different substances			
Abscisic acid and Potassium chloride	Anthesis	Achene and oil yield	Hussain et al. (2013a)
Abscisic acid	Bud initiation	Head diameter, Achenes per head, 1000-achene weight, Achene yield, Oil yield, Biological yield, Harvest index, Leaf area index, Crop growth rate	Hussain et al. (2014)
Abscisic acid	Bud and flower initiation	Oil yield and quality	Hussain et al. (2013b)
Foliar or root application of Salicylic acid and ascorbic acid	Vegetative and Reproductive stage	Mineral uptake	Ahmed et al. (2014)
Calcium chloride	30 and 50 days after sowing	leaf relative water content, leaf pigments, leaf minerals, organic osmolytes, phenolic related enzymes	Ibrahim et al. (2016)
Boron	Inflorescence emergence, flowering and seed filling	Achenes/head, achenes weight and achene yield	Shehzad et al. (2016)
Iron, Zinc, Copper and Manganese	Crop sowing	Antioxidant enzyme defence	Rahimizadeh et al. (2007)
Sodium nitroprusside as donor of nitric oxide	27 days after sowing	Piragalol peroxidase activity, Proline contents	Cechin et al. (2015)
Nitrogen and Potassium	Vegetative and Reproductive stage	Turgor maintenance, Enhanced accumulation of osmoprotectants, increased stomatal conductance and net photosynthesis, Reduced production of reactive oxygen species, Higher yield	Hussain et al. (2016)
Triazole compounds	30 days after sowing	Antioxidant enzyme defence, Growth, Biochemical potential	Rabert et al. (2014)
Zinc	Vegetative and Reproductive stage	Seed yield, Biological yield, Oil yield and Total chlorophyll	Robert et al. (2016)
Iron, Zinc and manganese	Inflorescence, Flowering and Grain Filling	Grain yield	Zafar et al. (2014)
Manures and synthetic fertilizers	Sowing	Nutrient uptake/concentration	Babaeian et al. (2011)
Silicon	Sowing	Leaf relative contents, Reduced membrane damage, Mineral/Nutrient uptake	Esmailian et al. (2012)
Glycinebetaine and Salicylic Acid	Vegetative and Reproductive stage	Head diameter, Number of achene, 1000-achene weight, Achene yield and Oil yield	Gunes et al. (2008a,b)
Glycinebetaine	Vegetative and Reproductive stage	Achene weight	Hussain et al. (2008)
Glycinebetaine	Vegetative and Reproductive stage	Achene yield	Iqbal et al. (2005)
Glycinebetaine	Vegetative and Reproductive stage	Achene yield	Iqbal et al. (2008)
Glycinebetaine	Vegetative and Reproductive stage	leaf endogenous levels of Glycinebetaine, soluble proteins and total soluble sugars	Iqbal et al. (2011)
Glycinebetaine and Salicylic Acid	Vegetative and Reproductive stage	Leaf area index, Leaf area duration, Crop growth rate, Leaf relative water contents, Water potential, Osmotic potential, Turgor pressure, Achene yield and Water use efficiency	Hussain et al. (2009a,b)

(2005) reported that moderate K deficiency promotes water uptake and reduces WUE in sunflower compare to well-watered plants. ABA regulation in K⁺ deficiency plants possibly prevents stomatal closure, increasing water uptake and transpiration. Moreover, the enhanced uptake in K⁺ starved plants might be attributed to the increase transpiration rate which forced the plant to extract more water from soil to maintain a water balance.

Application of micronutrients also improves the performance of sunflower under drought stress (Zafar et al., 2014; Babaeian et al., 2011; Rahimizadeh et al., 2007; Shehzad et al., 2016) by improving the antioxidant defense, stay green, achenes weight, achene yield, biological yield and oil yield. A 48–89% improvement in the production of antioxidant enzymes (SOD, CAT and GPX) with Fe + Zn + Cu + Mn application have been recorded in sunflower which indicates the significance of micronutrient application for improving the drought resistance of sunflower (Rahimizadeh et al., 2007; Babaeian et al., 2011). Significant improvements in physiological traits of drought stressed sunflower through Zn and CaCl₂ application have also been reported (Zafar et al., 2014). Recently, Ibrahim et al. (2016) reported positive effects of CaCl₂ foliar application on leaf relative water contents, leaf pigments (such as chlorophyll *a*, chlorophyll *b*, carotenoids, anthocyanins, carotenoids), leaf minerals (N, P, K and Ca), organic osmolytes

(proline and soluble sugars) and phenolic related enzymes such as phenylalanine ammonia lyase (PAL) and peroxidase (POD) in sunflower under drought stress.

Silicon application is also useful to reduce the drought induce yield losses in oilseed crops including sunflower. In a study, silicon application under drought stress improved the K, sulphur, magnesium, iron, copper, manganese; whereas the uptake of zinc remained unaffected (Gunes et al., 2008b). In another study, Gunes et al. (2008b) reported that exogenous application of silicon reduced leaf MDA, and enhanced the relative water contents, and the activities of enzymatic (e.g. catalase) and non-enzymatic antioxidant defense systems in sunflower (Gunes et al., 2008a). In a study on canola crop, the exogenous application of silicon increased the root/shoot dry weight, net assimilation rate, relative water contents, CO₂ absorbance, root amino acid contents, root water uptake, root proliferation, and the activities of superoxide dismutase and peroxidase (Habibi, 2014).

Organic manures are other viable option which improve drought tolerance when applied alone or in combination with synthetic fertilizers (Esmailian et al., 2012). These manures are beneficial source of major nutrients and affect the temporal dynamics of nutrient availability through improving soil physico-chemical properties (Paul and Beauchamp, 1993). Significant improvement in drought tolerance was

obtained when organic manure was applied to drought stressed sunflower either alone or in combination with synthetic fertilizers (Aowad and Mohamed, 2009). Similarly, organic manures both alone and in combination improved the nutrient uptake of sunflower under drought stress, which ultimately improved yield (Esmailian et al., 2012).

4.3.3. Arbuscular mycorrhizal fungi and polymers

The symbiotic relationship between plant roots and arbuscular mycorrhizal fungi is also an important strategy to improve mineral nutrition under abiotic stresses in plants (Brachmann and Parniske, 2006). Indeed, the arbuscular mycorrhizal fungi provides the surface area to plant roots to absorb water and nutrients (e.g. P, N, Zn, Cu) (Smith and Read, 2008). In a study, use of two species (i.e. *Glomus mossea* and *Glomus etanicatum*) of mycorrhiza improved the seed yield and seed nutrient contents in sunflower; *Glomus etanicatum* being more beneficial for improvement in seed yield and nutrient content of sunflower (Heidari and Karami, 2014). However, further studies are also needed to study the role of arbuscular mycorrhizal fungi for improving the performance of sunflower under drought stress under diverse environmental conditions.

Another way of improving the water use efficiency and achene yield of sunflower under drought stress is the use of super absorbent under arid and semi-arid climates. It has been reported that super absorbent polymers can hold ~400–1500 g of water per dry gram of hydro gel (Boman and Evans, 1991), thus increasing the water absorption and retention under drought stress. In a study, super absorbent polymer application at 2.25–3 g/kg of soil improved the water use efficiency under drought stress (Nazarli et al., 2010).

In conclusion, drought stress imbalances mineral nutrition, while use of macro- and micro nutrients, organic manures, arbuscular mycorrhizal fungi and polymers could possibly improve drought tolerance of sunflower through maintenance of nutrient balances.

4.3.4. Seed priming

Seed priming is a technique by which seeds are partially hydrated to a point where germination-related metabolic processes begin, but radicle is not emerged. Different seed priming techniques; hydropriming, salt priming, on-farm priming and chemical priming have been largely used for improving germination and crop establishment. Seed priming especially by osmopriming with KNO_3 and hydropriming improved the germination and stand establishment in sunflower crop both under stress (salt and drought) and normal conditions (Kaya et al., 2006; Hussain et al., 2006). Moghanibashi et al. (2012) also reported that hydropriming of sunflower seeds improved the germination percentage, germination index, root/shoot length and root/shoot dry weight of sunflower under drought stress. In another study, hydropriming of sunflower seeds improved the germination percentage, mean emergence time and seedling dry weight of two sunflower genotypes viz. Azargol and Hysun-36 (Sheidaie et al., 2013). Kausar et al. (2009) also found an improvement in seed vigour due to seed priming.

Biological priming of seeds is a developing technique which imparts tolerance to plants against various types of biotic and abiotic stresses (Singh et al., 2015). Significant improvements in drought tolerance of sunflower with biologically primed seeds with *Azotobacter chroococcum*, *Bacillus polymyxa*, alone or in combination have been reported (Singh et al., 2015). Both growth promoting bacteria significantly improved the activities of antioxidant enzymes, thus ameliorated the adverse effects of drought stress in sunflower. Gholamhoseini et al. (2013) found that inoculation of sunflower plants with two mycorrhizal fungi species viz. *Glomus mossea* and *G. hoi* improved the biomass, achene and seed yield in sunflower than non-inoculated plants.

It is concluded that seed priming; either chemical or biological, may help to improve the performance of drought stressed sunflower. Therefore, seed priming can be used to ameliorate the negative effects of drought stress on germination, growth and yield of sunflower to significant extent.

5. Conclusion and future directions

Drought stress affects the sunflower crop through its negative influence on seed germination, seedling growth, plant water relations, mineral nutrition, stay green, photosynthesis, transpiration, and grain partitioning thus affecting the seed yield and oil quality. However, various management practices including breeding for drought tolerance (conventional or biotechnological), exogenous application of hormones and osmoprotectants, seed treatment and soil nutrient management might be useful for improving drought tolerance in sunflower. The RNA mediated silencing and DNA methylation processes of specific genes are recent options explored in the developing era of functional genomics for improving abiotic stress tolerance in plants which can be successfully used for improving drought tolerance in sunflower. Several physiological parameters such as improved stomatal conductance, shoot and root dry weight, harvest index, root system, leaf hydraulics, and stay green are important physiological traits which needs to be considered when screening sunflower genotypes for breeding programs aimed on drought stress tolerance. For improving the water use efficiency of sunflower under drought stress, use of leaf carbon isotope discrimination technique, identification of QTLs responsible for efficient water use under drought stress and application of super absorbent might be quite beneficial. A comprehensive research on integration of different management options, including agronomic approaches, conventional breeding and modern biotechnological advances, is needed for the sustainable improvement of sunflower achene yield and oil quality under drought stress.

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