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REVIEW ARTICLE

Salt and drought stresses in safflower: a review

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Abstract Safflower is one of the oldest cultivated crops, usually grown at a small scale. Safflower is grown for flowers used for coloring, flavoring foods, dyes, medicinal properties, and livestock feed. Safflower is underutilized but gaining attention due to oil yield potential and the ability to grow under high temperatures, drought, and salinity. Salinity and drought have negative effects by disrupting the ionic and osmotic equilibrium of the plant cells. The stress signal is perceived by membranes then transduced in the cell to switch on the stress responsive genes. This review discusses on stress tolerance mechanisms in safflower. Strategies are proposed for enhancing drought and salt resistance in safflower.

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Keywords Compatible solutes · Drought stress · Growth · Salinity stress · Osmotic ionic · Stress tolerance · Management

Contents

1 Introduction

In addition to an increasing world population, there are several reasons for serious concern about sufficient future global production of food from crop plants. The availability of arable land is decreasing because of non-sustainable farming, soil erosion, soil degradation, and global climate changes (Rosegrant and Cline 2003; Lobell et al. 2008). Droughts, storms, floods, heat waves, and rises in sea level are predicted to occur more frequently, and salinity and other soil toxicities are likely to be much more problematic in some areas (Takeda and Matsuoka 2008). Comparing the effects of different stresses is an important step toward understanding plant behavior under realistic field conditions where stresses rarely occur alone (Voesenek and Pierik 2008). Salinity and drought are two of the most serious abiotic stresses, which pose a threat on crop productivity worldwide (Guo et al. 2014). According to an estimate, one third of the world's population live in areas where water is scarce (FAO 2003). Due to population growth and development of economic sectors, the competition for water resources will also grow (Laraus 2004). Drought is expected to increase in frequency and severity in the future as a result of climate change, mainly as a consequence of decreases in regional precipitation but also because of increasing evaporation driven by global warming (Lobell et al. 2008). Previous assessments of historic changes in drought over the late twentieth and early twenty-first centuries indicate that phenomena may already be happening globally (Sheffield et al. 2012). Drought affects more than 10 % of arable land, causing desertification especially in arid and semi-arid areas, while salinization is rapidly increasing on a global scale declining average yields for most major crops (Bray et al. 2000). According to the United Nations climatic report (http://www.solcomhouse.com/drought.htm), the Himalayan glaciers that feed to Asia's largest rivers (Ganges, Indus, Brahmaputra, Yangtze, Mekong, Salween, and Yellow) may disappear by 2035 due to rise in temperature. Under such circumstances, agriculture will be limited by reduced water supply and water of lower quality, particularly for crops with a water demand lower than that of horticultural or other intensive crops (Hsiao et al. 2007). Understanding plant resistance to drought and salinity is therefore of fundamental importance that can provide insights into the resistance mechanism against these abiotic stresses at biochemical, physiological, and molecular levels.

Recently, studies concerning resistance against drought and salinity in cultivated crops have been reported, while considerable advances have been made in this regard (Colmer et al. 2005). Therefore, salt-affected soils can be utilized by growing salt-tolerant plants, whether halophytes or non-halophyte crops (Rozema and Flowers 2008). However, it is imperative to explore intra-specific (inter-cultivar) variation for salt tolerance in a crop by screening its available germplasm. For instance, a great magnitude of inter-cultivar variation for salt tolerance has been observed in different crop species such as wheat (Ashraf and McNeilly 1988), lentil (Ashraf and Waheed 1990), barley (Belkhodja et al. 1994), cotton (Ashraf and Ahmad 1999), rapeseed (Ulfat et al. 2007), and safflower (Siddiqi et al. 2007; Fraj et al. 2013).

Safflower (*Carthamus tinctorius* L.) is one of the prospective oilseed crops because it yields about 32–40 % seed oil (Weiss 1971). However, due to its considerable salt resistance than commonly grown oilseed crops, it is cultivated in arid and semi-arid regions where soil salinity is one of the major threats to agriculture (Kaya 2009). Drought is very unpredictable among abiotic stresses in terms to occurrence, severity, timing. and duration (Chinnusamy et al. 2005), and safflower can be a promising alternate crop in dryland agro-ecosystems due to its growth potential under water stress without a substantial reduction of oil and seed yields (Kar et al. 2007). Safflower cultivation constitutes a more profitable crop for the farmers in some countries, compared to other conventional crops such as barley, lentil, and chickpea (Dajue and Mundel 1996; Yau 2004). The fact that safflower can overcome environmental stresses such as extreme temperatures, drought, and salinity has facilitated its expansion in areas around the world, where soil and climatic restrictions have impeded the cultivation of conventional food and cash crops (Yermanos et al. 1964; Weiss 2000). In particular, safflower has demonstrated drought resistance with a slight decrease in crop yield and significant stability in water use efficiency (Lovelli et al. 2007). The identification of adapted cultivars able to grow well in drought and saline environments may provide the germplasm for future breeding. Safflower petals are widely used as flavoring and food coloring agents and to prepare the textile dyes. Safflower has great potential as an oilseed, ornamental, medicinal, vegetable, and animal feed crop (Fig. 1). The meal obtained after oil extraction comprises considerable quantity of protein and is a favorite animal feed (Pavlov and Todorov 1996). Global production of safflower

Fig. 1 Safflower plants at growth, tillering, and reproductive stages (**a**, **b**), capitulum (**c**), and seeds (**d**). Photos: M. I. Hussain

exceeds 647 million tonnes, Kazakhstan and India being the leading producers (Fig. 2).

Salinity and drought stresses have become a significant problem in safflower production and management in many areas of the world. In order to conserve fresh water resources, non-potable water such as recycled, effluent or reclaimed water may become a major source of irrigation for safflower, particularly in semi-arid and arid areas (Tuck et al. 2006). Production and sustainable development of safflower require cultivars better able to perform well under drought and salinity stress. Understanding physiological mechanisms and molecular and genetic bases of tolerance against these stresses is critical for developing safflower germplasm and devising management strategies for profitable safflower production. In this review, we discuss the morphological, physiological, and biochemical responses of safflower to drought and salinity in order to better understand the limits and tradeoffs between the two stresses and explore how these responses can be exploited to improve drought and salinity tolerance. We also review the roles of exogenous protectants, mechanisms for transduction of salt and drought stress signals, transgenic approaches, and management strategies currently being taken to promote stress tolerance in safflower plants.

2 Effects

2.1 Drought

Drought is the single most critical threat to world food security. The severity of drought is unpredictable as it depends on many factors such as occurrence and distribution of rainfall, evaporative demands, and moisture storing capacity of soils (Wery et al. 1993). Three main mechanisms that reduce crop yield by soil water deficit include (i) reduced canopy absorption of photosynthetically active radiation, (ii) decrease in radiation-use efficiency, and (iii) reduced harvest index (Earl and Davis 2003).

Drought influences the crop production to a great extent. Plant species adaptable to regions suffering from water stress are sought in order to be incorporated in profitable agricultural production systems. Safflower is cultivated on marginal lands

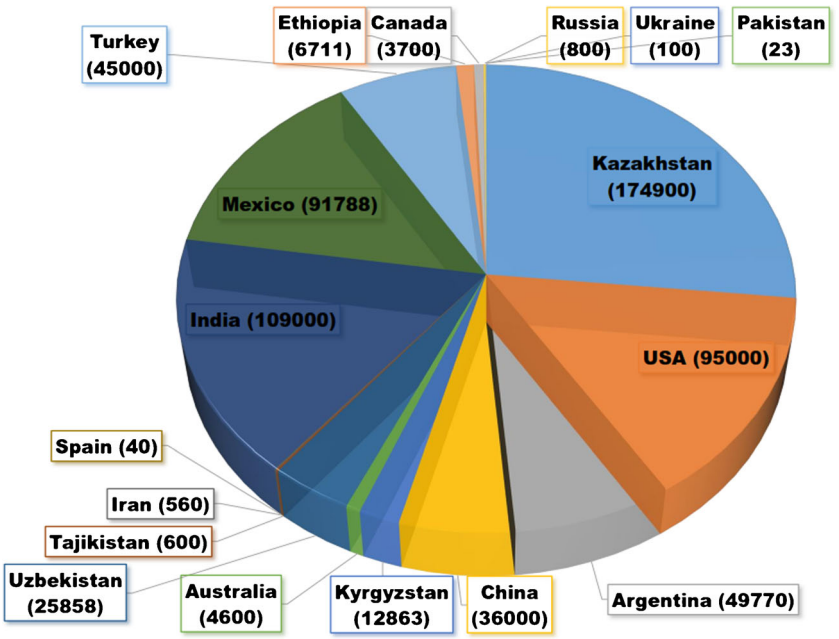

Fig. 2 Safflower production (thousand tonne) in different countries of the world. Source: FAO (2003)

that are relatively dry and has recently become popular for biofuel production (Dordas and Sioulas 2008). Safflower may uptake water from deep in the subsoil since it is characterized by a strong and deep taproot which facilitates its growth in dry climates (Dajue and Mundel 1996). The roots can grow to 2.2 m depth and its spines enable safflower plants to overcome drought hindrances. In the following lines, influence of drought stress on the growth and developmental cascades and physiological process responsible for yield formation has been presented.

2.1.1 Plant growth and development

Germination, vegetative, flowering, and seed filling stages of safflower are sensitive to water deficit. All the aforementioned developmental stages are influenced by a row of physiological responses, which may suppress plant growth and crop yield under drought. Germination is one of the most sensitive plant growth stages to water deficit (Farooq et al. 2009). Safflower germination and stand establishment were severely decreased under water deficit conditions (Sionit et al. 1973; Bassiri et al. 1977). However, combination of light and drought stress may increase the accumulation of polyphenol compounds in safflower seedlings, a desirable characteristic for the leaves that could be used as tea with anti-allergic and antioxidative properties (Yaginuma et al. 2002). Safflower is an extensively branching crop, and dry matter accumulation depends not only on plant height but also on branch development and morphological characteristics susceptible to drought stress (Koutroubas et al. 2004).

The qualitative and quantitative attributes of plant growth are the result of interactive phenomena among genetic, physiological, ecological, and morphological characteristics under drought conditions (Wang et al. 2003; Farooq et al. 2009). Vegetative stage constitutes a growth stage of vital importance for safflower when it is severely affected by water stress. Decreases in shoot length, shoot and root dry matter, and relative growth rate were observed for safflower varieties treated under water deficit conditions (Hojati et al. 2011). Deficit irrigation during the vegetative stage severely affected safflower production compared to full irrigation (Esendal et al. 2007). Decrease in growth rate under drought could be attributed to inhibition of cell elongation because the water flow is interrupted from the xylem to the surrounding cells (Nonami 1998). Furthermore, shoot growth seemed to be more adversely affected compared to root growth (Bassiri et al. 1977). Decrease in soil moisture causes decrease in seed germination, shoot length, and fresh and dry weights of safflower seedlings.

2.1.2 Plant water relations

Decrease in leaf water potential may provoke osmotic adjustment which helps maintain leaf hydration at low leaf water potential. Leaf relative water content and leaf water potential in safflower plants were affected by water deficit, whereas lipid peroxidation and antioxidant compound (ascorbic acid, α-tocopherol, reduced glutathione, superoxide dismutase, catalase, peroxidase) values were increased (Hojati et al. 2011). The leaf area index, chlorophyll content, and membrane stability indices in safflower plants were severely influenced by water deficit conditions, whereas substantial increase was provoked in antioxidant compounds, ascorbate peroxidase, and peroxidase (Amini et al. 2013). During seed filling stage, the drought stress exerted destructive consequences in relative water content, stomatal conductance, leaf temperature, osmotic adjustment, and leaf weight in five safflower genotypes (Pasban Eslam 2011).

2.1.3 Mineral uptake and assimilation

Drought stress also reduces the nutrient uptake by the roots and their translocation in the plant due to low transpiration rates, diminished active transport, and impaired membrane permeability (Hu and Schmidhalter 2005). Nitrogen (N) uptake, accumulation, partitioning, and translocation indices in safflower plants were affected by drier conditions prevailed in the second year of experimentation and as a result of significant N losses (Dordas and Sioulas 2009). Plant species and genotypes within a species may vary in their response to mineral uptake under drought stress (Garg 2003).

Phosphorus (P) addition was very important for plants under water deficit conditions since P uptake was reduced in dry-soil conditions. Symbiosis between the roots and mycorrhizae enhanced both the uptake of several elements including P and plant resistance exposed to growth. Total shoot N content was not affected in droughty safflower plants, while treated and untreated mycorrhiza safflower and wheat plants accumulated equal quantity of P in their leaves under drought conditions (Bryla and Duniway 1997).

2.1.4 Light harvesting and carbon fixation

Stress due to water limitations and stomatal closure imposes a negative impact on photosynthetic apparatus and diminishes thylakoid membranes, Calvin cycle enzyme activation ultimately decreased the plant growth and development (Ashraf and Harris 2013; Chaves et al. 2009; Farooq et al. 2009; Hussain and Reigosa 2011). Stomatal closure due to water deficit leads to a progressive limitation of photosynthetic carbon assimilation by causing changes in chlorophyll content by affecting chlorophyll contents (mainly *a* and *b*) and leading to photosynthetic apparatus collapse (Chaves 1991; Yordanov et al. 2000). The CO_2 limited availability due to stomatal closure may also induce an increase in sensitivity to photosystem II damage. In addition, the imbalance between reactive oxygen species

and antioxidant enzymes influences the photosynthetic potential of plants through higher oxidation of proteins, membrane lipids, and other cellular characteristics (Fig. 3; Farooq et al. 2009). Six safflower genotypes grown under drought stress were screened by Javed et al. (2013b) and compared to their oxidative damage and antioxidative responses. They reported that water stress reduced the chlorophyll *a* and *b* contents, but a decrease in chlorophyll contents was less in one safflower variety. Therefore, chlorophyll contents could demonstrate a useful marker for selecting a stress-tolerant variety.

Chlorophyll, xanthophyll pigments, and carotenoids constitute an important indicator, which can be used to measure chlorophyll loss in plants under environmental stresses (Hussain and Reigosa 2011, 2014, 2015). Amini et al. (2013) evaluated 64 safflower genotypes under water deficit conditions and observed that cultivars with low seed yield were characterized by low chlorophyll values.

2.1.5 Seed, oil yield, and quality

Translocation of pre-anthesis assimilates to the seed is a crucial physiological process during the filling phase of safflower seeds, especially under drought. The high seed filling rate is a very important characteristic for selection of safflower genotypes to increase yield in arid regions (Koutroubas and Papakosta 2010). Filling rate is dependent on current photosynthesis, dry matter redistribution from vegetative tissues to the seeds during the filling period as well as by the sink size (Koutroubas and Papakosta 2010). Storage of pre-anthesis assimilates has great significance to obtain higher yield (Koutroubas et al. 2004). The prevalence of hot and dry conditions during the maturity phase influenced the rate of photosynthesis, nitrogen assimilation, and the sink size of safflower seeds. As a result, biotic and abiotic stresses diminish photosynthesis and crop nitrogen uptake limiting safflower production (Koutroubas and Papakosta 2010).

Typically safflower seeds contain 30–40 % oil, 15–20 % protein, and 35–45 % hull (Rahamatalla et al. 2001). Distribution and composition of fatty acids in safflower seeds in variable and ordinary seeds contain about 2–3 % stearic acid, 16–20 % oleic acid, 6–8 % palmitic acid, and 71–75 % linoleic acid (Nagaraj 1993). In comparison, high linoleic safflower varieties contain 87–89 % linoleic acid and high oleic acid varieties constitute over 85 % oleic acid. In recent years, safflower has become a major oilseed crop with good oil and fatty acid composition (Çamaş and Esendal 2006; Yeilaghi et al. 2012). Safflower oil contains a large amount of unsaturated fatty acid; however, the composition of the oil was not affected by drought. However, drought reduces the palmitic, stearic, oleic, and linoleic acid contents (Ashrafi and Razmjoo 2010).

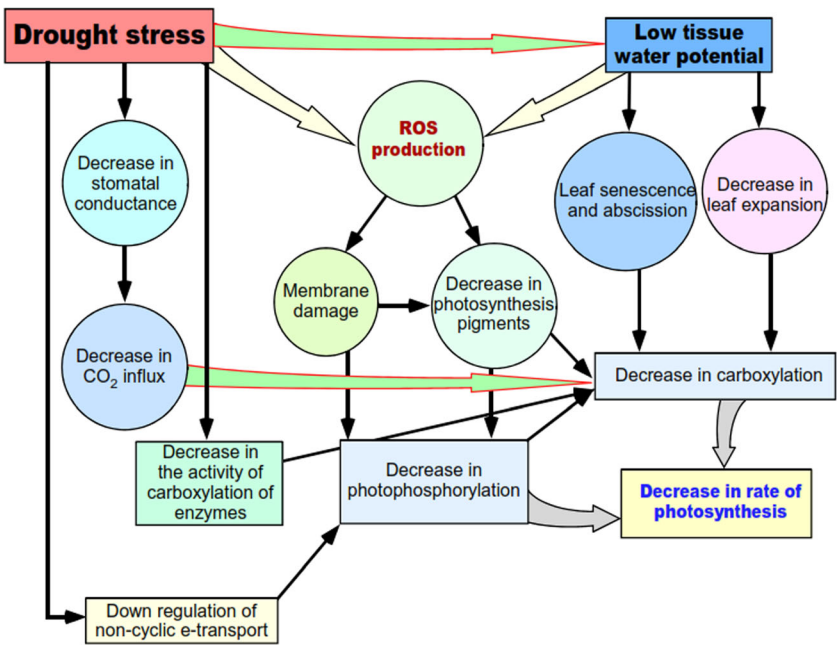

Fig. 3 Influence of drought stress on photosynthesis. Drought stress lowers the tissue water status, which suppresses the leaf development and accelerates the leaf senescence and abscission resulting in decrease in photo-assimilatory size, and thus, carboxylation is decreased. Drought disturbs the balance between the production of reactive oxygen species (ROS) and the antioxidant defense causing accumulation of ROS, which induces oxidative stress. Drought also induces stomata closure, which decreases the CO_2 influx. Reduction in CO_2 not only reduces the carboxylation directly but also directs more electrons to form ROS. Under severe drought, activities of carboxylation enzymes are reduced. Under drought stress, non-cyclic electron transport is downregulated to match the reduced requirements of NADPH production and thus reduces the rate of photophosphorylation. Conceived from Farooq et al. (2009)

Istanbulluoglu et al. (2009) observed that when irrigation was omitted for winter and summer sowings during vegetative stage, yield response factor was decreased. In water-constrained regions, winter sowing is suggested more productive than summer to maintain high yield of oil production. Anthesis is a very sensitive stage to drought (Movahhedy-Dehnavy et al. 2009). Any episode of drought during flowering period, irrespective of sowing time, may cause substantial decrease in seed yield (Yau 2007). Drought during flowering and seed filling stages, in spring safflower plantations, caused decrease in yield and yield attributes (Koutroubas et al. 2009; Yau 2007). Reduction in the number of seeds, flower numbers per capitulum, and head fertility was observed under drought and late sowing (Cazzato et al. 1997). Safflower seed yield is negatively influenced by drought particularly in flowering and heading (Zarghami et al. 2011). Similarly, drought at heading stage decreases the foliage chlorophyll content together with seed and oil yield (Kafi and Rostami 2008). Antioxidant and oil contents of safflower genotypes from diverse origin grown under normal and water deficit conditions are elaborated in Table 1. Safflower translocates 65–92 % of its pre-anthesis storage assimilates to the seed during late season drought (Koutroubas et al. 2004). Safflower oil content was influenced by different irrigation regimes (Ashrafi and Razmjoo 2010). Lovelli et al. (2007) showed that the harvest index in safflower did not significantly change in five irrigation regimes with a restoration of 100, 75, 50, 25, and 0 % of the maximum crop evapotranspiration, but seed yield declined sharply under severe drought stress.

Safflower seed oil contains a large amount of saturated (palmitic and stearic) and unsaturated (oleic, linoleic, and linolenic) fatty acids, and composition may be affected by abiotic stresses (Dajue 1993; Sabale and Deokar 1997; Fernández-Cuesta et al. 2014). Ashrafi and Razmjoo (2010) reported that the oil contents of safflower cultivars were significantly reduced due to drought stress. In particular, both the stearic and palmitic acid contents were reduced by 57 % on average, whereas the linoleic and oleic acid contents were reduced by only 8 and 14 %, respectively. The results clearly showed that water deficit conditions severely affected saturated compared to unsaturated fatty acid contents. Drought, occurring in the late flowering and seed filling stages in spring safflower genotypes, decreased seed and oil production, mainly by decreasing yield components such as the number of seeds in the capitulum, the 1000-seed weight and harvest index (Eslam et al. 2010). Oil yield constitutes a combination of seed yield and oil content. Koutroubas et al. (2009) observed that the ranking among safflower genotypes for oil yield was similar to that of seed yield because the oil yield was mainly determined by seed yield.

2.2 Salinity

2.2.1 Osmotic effects

Salt accumulation in the soil reduces the water potential of soil solution which adversely affects plant water conductance and ultimately plant tissue water content (Munns 2002). High accumulation of salts in saline soils results into reduced water potential of soil solution which causes difficulty for plants to extract water from soil experiencing "osmotic stress." The excess salts reduce plant growth primarily because these bulk salts increase the utilization of energy that the plant must use to acquire water from the soil and to make biochemical adjustments. This energy is diverted from the processes that lead to reduced growth and yield of plants (Akram et al. 2002). Salt stress suppressed the leaf water relation parameters, relative leaf water content, water potential, osmotic potential, turgor potential, and ultimately decreased the safflower fresh weight and inhibited plant growth (Jabeen and Ahmad 2012).

Leaf water and osmotic potential decreased under salinity stress, but they were less affected in the salt-tolerant ecotypes than the sensitive ecotypes in safflower (Gadallah 1996; Gadallah and Ramadan 1997; Hameed and Ashraf 2008; Yermanos et al. 1964). Under stress, osmotic potential of the soil solution become low and the seed germination will be inhibited due to difficulty in water absorption by seeds and casing sodium toxicity to embryo under alteration (Hasegawa et al. 2000; Farsiani and Ghobadi 2009). Salinity decreased the germination percentage, germination rate, shoot, root and seedling length, root/shoot length ratio, seed vigor, and germination index in all the six genotypes of safflower while cultivar "Kose" was more resistant while cultivars KM5, KM8, and KM47 were sensitive genotypes (Khodadad 2011). The reduction in growth can be considered as a possibility to preserve carbohydrates for sustained metabolism, prolonged energy supply, and better recovery after stress relief. Mild salinity stress leads rapidly to growth inhibition of leaves and stems, whereas roots may continue to elongate (Spollen et al. 1993).

2.2.2 Specific ion toxicity

Specific ion toxicity, the result of excessive uptake of certain ions is the primary cause of growth reduction under salt stress (Chinnusamy et al. 2005). Toxic ions in salt-affected soils are usually sodium, chloride, and sulfate (Ghassemi et al. 1995; Munns and Tester 2008). The excessive sodium ion (Na^+) accumulation causes ion toxicity and interferes with plant metabolism while accumulation of potassium ion (K^+) can alleviate Na^+ toxicity by adjusting osmotic potential and through ion balance. It has been reviewed that high Na^+ accumulation causes greater damage in leaves as compared to those in roots

Table 1 Antioxidant and oil contents of safflower genotypes from diverse origin grown under normal and water deficit conditions

Genotypes	Origin	Catalase (nmol min^{-1} mg protein)		Ascorbate peroxidase (nmol min^{-1} mg protein)		Peroxidase (nmol min^{-1} mg protein)		Carotenoids (mg g^{-1} fw)		Seed yield (kg ha^{-1})		Protein content (%)		Oil content (%)		Oil yield (kg ha^{-1})	
		Normal	Stress	Normal	Stress	Normal	Stress	Normal	Stress	Normal	Stress	Normal	Stress	Normal	Stress	Normal	Stress
C111	Iran	1.99	2.49	0.40	1.82	0.22	3.30	0.20	0.20	1986.20	1026.90	15.70	15.50	28.90	25.34	574.10	260.20
C116	Iran	1.52	1.85	27.00	1.66	3.92	7.11	0.23	0.22	1781.30	1349.10	14.30	15.31	27.38	23.85	513.80	323.10
C411	Iran	3.10	1.63	0.42	1.75	0.51	11.10	0.20	0.17	2555.50	2530.70	15.75	20.76	26.78	22.65	610.10	574.10
C444	Iran	1.40	0.63	0.45	1.47	3.05	6.48	0.22	0.22	1795.10	783.30	20.90	21.52	28.86	26.75	525.30	210.40
C4110	Iran	1.69	2.84	0.41	1.88	1.59	2.67	0.21	0.19	2089.20	1149.60	19.45	17.31	28.01	26.50	593.00	304.10
S6-58/41-168	Iran	2.96	2.20	0.31	1.57	0.85	6.54	0.20	0.21	2172.50	1269.60	14.25	17.52	26.78	23.45	583.40	296.80
S6-697-307	Iran	1.62	3.20	0.39	1.80	1.19	5.10	0.26	0.22	1785.20	1128.50	14.45	16.51	29.61	27.75	525.30	313.20
S6-697-324	Iran	1.85	4.48	0.69	1.74	6.72	3.55	0.24	0.13	1972.00	1640.30	16.75	16.59	26.71	25.10	472.10	412.80
IL	Iran	1.44	2.64	0.31	1.75	0.85	5.86	0.25	0.22	3025.50	2308.40	18.35	21.32	27.70	22.45	833.80	516.90
N/27	Iran	2.84	0.26	0.47	1.78	1.21	4.21	0.23	0.21	1686.60	875.40	16.25	19.57	27.72	25.65	467.90	225.10
73-14-34	Iran	3.38	2.86	0.42	1.78	1.95	2.94	0.23	0.19	1790.20	1360.20	17.60	15.30	27.80	27.00	499.80	362.10
PI-405985	Iran	2.56	0.77	0.39	1.76	1.19	3.17	0.22	0.18	1432.30	806.10	16.20	18.81	25.38	23.26	363.70	190.10
LRV-51-51	Iran	1.41	1.41	0.25	1.76	0.95	7.97	0.23	0.20	1829.40	1505.50	15.05	15.70	27.60	26.05	497.20	392.70
LRV-55-295	Iran	2.61	0.94	0.52	1.58	3.20	3.08	0.22	0.17	2138.20	1641.70	16.65	18.18	28.42	25.85	606.20	424.50
Hamedan17	Iran	1.68	2.86	0.35	1.76	1.90	3.70	0.20	0.21	2050.00	1451.90	17.20	15.82	32.95	31.05	668.30	447.10
Hamedan21	Iran	2.42	1.71	0.45	1.55	1.11	6.04	0.24	0.21	2473.50	1793.20	14.40	16.10	27.55	26.81	674.10	483.00
Hamedan38	Iran	1.55	0.35	0.36	2.04	2.33	9.13	0.19	0.12	2520.50	2128.00	16.35	20.50	29.97	22.80	758.80	480.40
Hamedan40	Iran	1.72	1.34	0.60	1.61	5.10	6.55	0.24	0.26	1496.00	1062.60	15.40	15.80	28.33	25.05	510.00	266.10
Kordestan1	Iran	1.80	2.79	0.62	1.62	6.83	5.35	0.18	0.16	2417.90	1977.90	19.65	20.25	29.90	28.50	644.70	569.20
Kordestan2	Iran	2.25	0.26	0.90	1.76	4.31	6.41	0.24	0.21	1834.30	1505.20	16.25	18.45	28.29	26.45	513.40	395.20
Kordestan3	Iran	1.68	4.48	0.47	2.62	6.20	8.14	0.25	0.23	1822.50	2161.00	17.15	20.10	29.04	26.40	453.60	475.80
Kordestan4	Iran	3.27	1.12	0.31	2.05	0.58	7.33	0.24	0.19	1613.70	945.40	18.95	17.70	25.19	22.80	404.60	296.30
Kordestan5	Iran	2.78	1.67	0.98	2.11	1.56	5.68	0.19	0.16	2494.10	1959.80	20.10	21.82	27.99	24.95	692.60	491.10
Kordestan6	Iran	1.84	2.08	0.36	1.71	4.42	2.63	0.23	0.13	2240.00	1391.60	18.25	19.55	28.40	25.35	627.50	355.90
Kordestan7	Iran	2.63	3.29	0.40	1.93	1.36	4.09	0.18	0.17	1901.90	1275.00	13.56	15.45	26.97	23.85	516.80	299.10
Kordestan8	Iran	1.08	1.00	0.48	1.68	3.12	3.68	0.21	0.22	1990.60	1787.70	15.15	16.40	30.24	26.95	495.50	478.40
Kordestan9	Iran	1.05	2.19	0.29	1.82	3.42	4.44	0.20	0.21	2103.90	1485.50	15.95	17.22	27.65	24.25	580.20	337.50
Darab1	Iran	3.04	2.80	0.54	1.62	1.76	3.63	0.21	0.17	1677.40	1025.30	16.30	17.24	27.05	25.65	454.20	265.80
Darab2	Iran	3.08	2.75	0.61	1.15	0.90	3.17	0.20	0.23	2099.00	1460.20	14.60	16.87	26.73	25.10	565.50	365.40
Darab4	Iran	3.97	3.35	0.54	1.78	4.16	2.40	0.22	0.21	2092.10	1160.20	15.95	17.86	27.98	23.35	587.50	272.30
Darab9	Iran	1.34	2.96	0.51	1.62	3.96	2.06	0.23	0.20	1839.20	1085.70	14.35	19.95	29.40	26.10	552.30	281.80
Khorasan62	Iran	1.88	2.40	0.61	1.76	5.58	4.96	0.24	0.17	3100.00	1729.70	16.65	18.16	30.37	27.45	934.70	476.50
Khorasan330	Iran	2.04	2.10	0.37	1.98	0.39	4.44	0.23	0.20	2323.50	1258.80	15.55	17.36	28.52	27.20	667.30	337.30

Table 1 (continued)

Genotypes	Origin	Catalase (nmol min^{-1} mg protein)		Ascorbate peroxidase (nmol min^{-1} mg protein)		Peroxidase (nmol min^{-1} mg protein)		Carotenoids (mg g^{-1} fw)		Seed yield (kg ha^{-1})		Protein content (%)		Oil content (%)		Oil yield (kg ha^{-1})	
		Normal	Stress	Normal	Stress	Normal	Stress	Normal	Stress	Normal	Stress	Normal	Stress	Normal	Stress	Normal	Stress
Khorasan376	Iran	2.19	1.88	0.52	1.58	3.91	3.04	0.21	0.20	2321.50	1187.80	14.90	16.95	29.02	25.85	676.10	306.30
Khorasan508	Iran	2.72	2.68	0.65	2.11	1.91	3.54	0.23	0.21	1574.20	1508.40	13.40	15.40	29.50	27.05	457.40	407.10
Kermanshah	Iran	2.10	1.56	0.45	1.65	1.11	2.27	0.24	0.21	1676.40	1069.60	15.95	16.89	28.20	28.45	705.80	459.70
Kermanshah44	Iran	3.37	1.58	0.44	1.87	1.48	3.00	0.21	0.23	1813.70	767.20	14.55	17.17	28.60	25.30	522.60	267.20
Kermanshah46	Iran	3.23	0.76	0.43	1.51	0.44	3.31	0.24	0.22	1749.00	940.10	13.10	16.81	27.87	25.30	482.80	237.30
Kermanshah47	Iran	3.66	3.66	0.34	2.07	2.56	4.10	0.21	0.22	3574.50	1792.60	19.00	18.10	24.63	21.65	885.70	469.40
Kemanshah60	Iran	3.07	1.93	0.60	2.07	1.93	3.26	0.26	0.19	1476.40	1117.80	15.55	16.37	26.51	24.45	376.90	275.70
Esfahan4	Iran	2.55	1.54	0.59	1.98	5.00	7.85	0.22	0.20	1878.40	1748.20	17.95	16.85	27.83	28.00	514.50	473.10
Esfahan kuse	Iran	2.72	1.49	0.29	1.60	3.40	3.23	0.25	0.15	1805.60	1310.00	17.80	20.22	25.28	23.85	423.50	314.60
Marand	Iran	2.52	1.94	0.88	1.62	5.91	3.73	0.24	0.19	1564.70	1060.00	14.65	14.17	27.56	25.20	439.10	268.40
Zarghan	Iran	2.48	2.13	0.40	1.86	0.41	7.48	0.21	0.19	2133.30	1539.90	15.85	15.43	26.51	25.15	571.60	387.80
Sina	Iran	1.33	3.61	0.70	2.05	7.91	5.10	0.21	0.17	1858.80	1716.10	15.05	17.33	28.66	27.25	536.30	471.60
Arak	Iran	1.40	2.24	0.50	1.59	4.66	4.93	0.20	0.20	1580.30	1458.40	18.90	18.25	25.24	25.30	386.90	368.70
Dincer	Turkey	4.45	3.53	0.57	1.82	1.51	4.99	0.18	0.20	2694.10	1197.70	21.25	15.42	27.57	23.35	589.40	282.80
Yinice	Turkey	2.24	1.70	0.62	1.96	2.93	2.63	0.23	0.22	2499.00	1470.50	15.90	15.65	29.63	27.80	741.80	411.20
C1055	Turkey	2.57	0.57	1.13	1.54	1.21	4.71	0.26	0.17	2285.20	1482.80	16.00	17.04	30.70	26.99	703.80	397.60
PI-198844	France	2.54	1.62	0.36	1.74	2.51	7.98	0.24	0.19	2311.70	1388.20	14.10	18.34	27.50	25.05	544.90	376.80
PI-253384	Palestine	3.32	2.32	0.57	1.78	7.41	5.51	0.19	0.18	2018.60	1877.90	19.05	17.31	24.42	22.75	455.70	425.60
PI-250190	Pakistan	2.42	3.40	0.44	1.78	1.09	2.75	0.13	0.21	1811.70	1541.70	16.30	18.83	28.34	27.05	494.60	422.10
PI-250537	Egypt	2.87	4.06	0.32	1.76	4.13	4.40	0.18	0.19	2211.70	1606.80	14.55	20.79	27.67	24.95	599.50	401.10
PI-506426	China	2.88	2.44	0.54	1.86	1.70	4.17	0.16	0.20	2103.90	1402.90	13.90	18.21	32.15	26.65	866.70	373.90
Cyprus Bregon	Cyprus	3.30	1.83	0.53	1.58	3.54	4.62	0.19	0.20	1804.90	1227.20	15.70	15.25	28.17	25.80	557.30	315.70
Syrian	Syria	4.18	1.88	0.36	1.65	1.38	6.68	0.23	0.23	2394.10	2060.40	13.00	12.86	26.87	23.00	636.70	476.50
PI-258417	Portugal	3.94	1.58	0.37	1.65	7.61	6.50	0.22	0.20	1804.90	1507.90	15.30	19.89	28.44	25.30	513.50	383.90
Hartman	USA	1.56	2.92	0.34	1.84	1.60	2.78	0.21	0.20	2476.40	1629.80	16.60	12.36	28.93	26.05	490.80	202.10
Gila	USA	2.03	0.43	0.53	1.83	3.44	6.33	0.21	0.18	1648.00	1274.10	14.20	20.18	27.97	26.55	509.20	252.90
CW-4440	USA	2.76	0.78	0.65	1.12	1.50	1.97	0.20	0.21	1741.10	1125.00	13.90	13.77	31.41	27.99	541.70	316.10
S-541	USA	2.14	3.31	0.51	1.86	4.54	6.10	0.18	0.21	2392.10	1083.90	14.70	17.02	29.70	26.75	728.80	288.30
PI-537636-S	USA	2.62	0.94	0.44	1.60	3.23	4.21	0.23	0.15	1790.20	925.80	17.40	14.89	27.28	25.80	417.30	239.10
PI-537636	USA	3.40	1.44	0.34	1.89	1.07	7.62	0.19	0.17	1922.50	1013.00	19.70	16.45	28.60	27.25	514.70	277.30
Kino-76	Mexico	0.93	2.04	0.44	1.53	3.31	9.26	0.18	0.18	1643.80	1431.60	12.45	17.54	27.78	26.45	443.50	381.60

Source: Amini et al. (2014)

(Munns 2002, 2005), and burning of leaves is a major symptom (Zhu 2003).

Many physiological studies have demonstrated that Na^+ toxicity is not only due to toxic effects of Na^+ in the cytosol but also because K^+ homeostasis is disrupted possibly due to the ability of Na^+ competing for K^+ binding sites. The chloride uptake was stimulated at all levels of chloride and sulfate salinization in *Carthamus tinctorius* cv. Bhima, and concentrations were more in the roots which reflected that the salt tolerance mechanism of this variety is associated with exclusion of chloride ion (Cl^-) from leaves (Ashraf and Fatima 1995). Sodium and sulfate stimulated sulfate uptake, which reflects that plants have the ability to maintain sulfate uptake under saline conditions (Patil 2012). Increased NaCl resulted in an increase in the Na^+ and Cl^- content of the seedlings, while the K^+ content was not affected and large size seeds produced vigorous seedling growth due to a lower ion accumulation under NaCl stress (Kaya et al. 2011).

2.2.3 Imbalances in mineral uptake and assimilation

Crop performance may be adversely affected by salinity-induced nutritional imbalances (Hu and Schmidhalter 1998). These imbalances may result from the effect of salinity on nutrient availability, competitive uptake, transport, and/or partitioning within the plant caused by physiological inactivation of a given nutrient resulting in increased plant's internal requirement for that essential element (Marschner 1995). In salt-affected soils, excessive buildup of Na^+ and Cl^- ions in the rhizosphere leads to severe nutritional imbalance in safflower due to strong interference of these ions with other essential mineral elements such as potassium (K), calcium (Ca), nitrogen (N), phosphorus (P), magnesium (Mg), iron (Fe), manganese (Mn), copper (Cu), and zinc (Zn) (Hu and Schmidhalter 1998; Siddiqi et al. 2011). Na^+ is the principal toxic ion, which interferes with potassium uptake and transport in safflower leading to disturbance in stomatal modulations and causing water loss and necrosis (Siddiqi et al. 2011). Competition between potassium and sodium under salt stress severely reduces potassium content in both leaves and roots of safflower (Kaya et al. 2011). The uptake of phosphate and its accumulation is reduced in crops due to salt stress due to the reduced availability of phosphate in salt-affected soils (Ashraf 2004). Increase in Na^+ and Cl^- levels in rhizosphere may induce strong competition with other essential minerals such as K^+, Ca^{2+}, and NO_3^- and may thus inhibit their uptake (Hu and Schmidhalter 2005). The accumulation of Ca^{2+}, K^+, and N was decreased with increase in salt stress (Jamil et al. 2006) and Ca^{2+} displaces Na^+ from the plasmalemma of salt-stressed root cell, thus decreasing the influx of ions into the cytoplasm (Lynch et al. 1987). P contents were higher than control at all levels of NaCl and Na_2SO_4, indicating that P uptake is stimulated in safflower cv. Bhimawhichisone (Patil 2012).

Increased sodium accumulation also disturbs Zn nutrition in plants. The high concentration of Zn in safflower improved the growth of roots and enhanced xylem development in NaCl-stressed plants compared with plants grown without Zn (Gadallah and Ramadan 1997). The Zn contents in roots were decreased with increased salt in level; whereas in stem and leaves, Zn content increases in safflower with increasing salinity (Patil 2012). The Fe^{+2} uptakes were stimulated at all levels of salts in safflower cv. Bhima, and Fe^{+2} is not much stored in roots but it is translocated to the stem. Within the stem, Fe^{+2} is more retained under salinization indicating the presence of some regulatory mechanism within the stem.

2.2.4 Light harvesting and carbon fixation

Photosynthesis is the most important process by which green plants convert solar energy into chemical energy in the form of organic compounds synthesized by fixation of atmospheric carbon dioxide. Photosynthesis is adversely affected by salinity in various ways, such as the inhibition of CO_2 intake with stomatal closure (Degl'Innocenti et al. 2009), the reduction of photosynthetic pigment, chlorophyll *a* and *b* (Qados 2011), and damage to photosynthetic processes (photosystems I and II, electron transport proteins (Sudhir et al. 2005)). The reduction in photosynthesis due to salt stress is partly ascribed to reduction in chlorophyll contents (Ashraf 2004). The salt stress significantly reduced the chlorophyll *a* and *b* of safflower accessions, and some accessions were salt tolerant (safflower-35, safflower-36, safflower-38, and safflower-39) while others (safflower-31 and safflower-34) were salt sensitive (Siddiqi et al. 2009).

Total photosynthesis decreases due to inhibited leaf development and expansion, as well as early leaf abscission, and as salt stress is prolonged, ion toxicity, membrane disruption, and complete stomatal closure become the prime factors responsible for photosynthetic inhibition (Fig. 4; Farooq et al. 2015). Munns and Tester (2008) identified the reduction in stomatal aperture as the most dramatic and readily measurable whole-plant response to salinity and concluded that the osmotic effect of salt outside the roots induces stomatal responses. Salt stress affects stomatal conductance immediately due to perturbed water relations and shortly afterward due to the synthesis of abscisic acid. Salinity and drought decreased the chlorophyll contents in safflower variety "THORI-78" in a net house trial (Javed et al. 2013b). Reduction in chlorophyll contents under salt stress can be due to deterioration of pigment protein complexes (Singh et al. 1990). The rate of photosynthesis, biomass, and seed yield was decreased with increase in salinity (Siddiqi et al. 2009). Salinity can reduce the photosynthetic activity and is usually caused by decreased stomatal conductance, which reduces transpiration rate but also CO_2 uptake

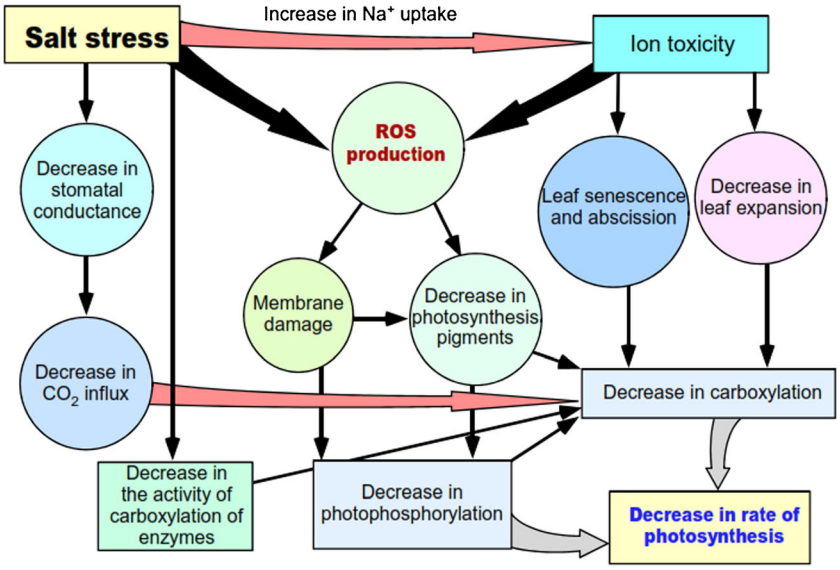

Fig. 4 Influence of salt stress on photosynthesis. Under salt stress, uptake of Na^+ increases resulting in increase in tissue Na^+, which causes decrease in leaf growth and induces early leaf abscission. Salt stress disturbs the balance between production of reactive oxygen species (ROS) and antioxidant defense causing accumulation of ROS, which induces oxidative stress. Salt stress also induces stomata closure, which decrease the CO_2 influx. Reduction in CO_2 intake reduces the carboxylation rate. Under severe salt stress, activities of carboxylation enzymes are also reduced. Conceived from Farooq et al. (2015)

(Iyengar and Reddy 1996). In safflower, following salinity treatment lowered the transpiration rate, altered leaf cell structure, and decreased stomatal numbers (Devi et al. 1980; Weiss 1971).

2.2.5 Seed, oil yield, and quality

Soil salinization and alkalization affect the soil productivity and quality of crop plants in arid and semi-arid areas of world. Suitability of vegetable oil for human consumption depends upon the composition of fatty acids in oilseed crop. Although safflower is produced on marginal lands, its oil is still considered an ideal in terms of fatty acid composition. However, salt stress could have a negative impact on oil contents in various safflower cultivars (Bassil and Kaffka 2002; Irving et al. 1988). Moreover, salt stress decreased the number of capitula per plant, number of seeds per capitula, and seed oil contents (Irving et al. 1988). Safflower crop is more sensitive to salinity at germination stage in comparison to late development stages, the plants have small height with reduced stem diameter, and the plants are more succulent with thick and darkened leaves (Weiss 1971; Beke and Volkmar 1995; Bassil and Kaffka 2002). However, the fatty acid composition of safflower linoleate oil was not affected by increasing salinity, while fatty acid composition was altered in the high-oleate cultivars, resulting in decreased oleic acid contents (Irving et al. 1988).

Yeilaghi et al. (2012) reported a significant reduction in safflower seed yield, oil contents, and fatty acid composition in 64 safflower genotypes following salinity treatment. Moreover, salt stress caused a significant increase in oleic acid and decrease in linolenic acids in different safflower genotypes. Safflower seed and oil yield were not affected with increase in electrical conductivity of soil, but the oil content and 1000-seed weight were increased slightly with increase in soil salinity (Bassil and Kaffka 2002). Siddiqi et al. (2011) found a decrease in seed yield, number of seed per capitula, and 1000-seed weight while α-tocopherols, stearic, oleic, and linoleic acid contents were not affected. The application of 50 mM NaCl decreased the total lipid contents in both roots and aerial parts with great variations in the fatty acid profile. The major changes in fatty composition were an increase in palmitic, oleic, and linoleic acids; however, an opposite trend of linolenic acid was observed between roots and aerial parts (Harrathi et al. 2012).

3 Resistance mechanism

Drought constitutes a multidimensional stress that impairs the phenological, morphological, physiological, biochemical, and molecular status of plants and ultimately affects the crop growth and production (Bartels and Sunkar 2005; Farooq et al. 2009; Wang et al. 2003; Yordanov et al. 2000). Drought escape, solute accumulation, antioxidant defense, photosynthesis, and changes in the hormonal profile are the most important strategies deployed by the plant to combat water deficit conditions.

Responses of plants to soil salinity are also complex and include stress sensing and signaling, ion homeostasis, osmoregulation, detoxification, and growth regulation (Munns and

Tester 2008; Zhu 2001). At the metabolic level, plants may display changes in phytohormones, accumulation of osmolytes (soluble sugars, amino compounds), and increases in membrane lipid oxidation in response to salinity within an hour to several days of stress exposure (Bolu and Polle 2004).

3.1 Drought

3.1.1 Drought escape

Plants adopt various strategic tactics to cope with water deficit conditions such as escape, avoidance, and tolerance (Rasool et al. 2013). Plants may complete their growth cycle before the onset of the dry months owing to increase in metabolic activity and rapid growth or they may alter their phenotype by increasing escape traits under drought conditions (Sherrard and Maherali 2006). Although safflower is considered to be one of the most xeric crops of all oilseed annual worldwide that can sustain dry conditions, its yield was decreased because of late sowing of rainfed safflower in a semi-arid Mediterranean environment (Yau 2007). In this case, low seed yield may be attributed to less precipitation, diminished biomass production, and late flowering in plants that are more vulnerable to terminal drought and heat. Safflower could be grown as a winter crop in areas with temperate climate or as spring crop in areas characterized by cooler temperatures. However, autumn plantation compared to spring sowing led to a significant increase in seed production (Koutroubas et al. 2004; Mündel et al. 1994; Yau 2007). A great disadvantage for safflower grown in locations with Mediterranean-type climate is that irrespective of sowing time, anthesis stage falls into summer months when high evapotranspiration values are denoted and drought period starts (Corleto et al. 1997; Koutroubas et al. 2009).

3.1.2 Solute accumulation

Plants that undergo water deficit conditions need to maintain water potential below that of soil through overproduction of compatible organic solutes (Serraj and Sinclair 2002). Low molecular weight solutes are accumulated in the cytoplasm so that the osmotic potential decreases and is maintained below that of the soil so that water uptake can be facilitated (Ahmad et al. 2008). Such organic solutes protect plants from stressful conditions contributing to osmotic adjustment, withdrawal of reactive oxygen species (ROS), membrane stabilization, and structural characteristics of proteins and enzymes (Farooq et al. 2009). The majority of the osmotically active molecules that are accumulated in the cell include amino acids (proline, glycine betaine, etc.), sugars (trehalose, glucose, raffinose and fructose), sugar alcohols (glycerol), and sulfonium compounds. Among the abovementioned cytosolutes, proline and glycine betaine constitute the most important organic solutes that have a multifunctional role in plants' defense, combating stresses.

Plant genotypes tolerant to abiotic stresses such as drought and excessive salinity demonstrate high proline concentrations, which is often correlated with elevated stress tolerance (Ahmad et al. 2012). Four safflower genotypes (Esfahan native, Esfahan-14, PI537, 598, and IL111) were evaluated for the biochemical responses under water deficit conditions (Sajedi et al. 2012). The first two cultivars were characterized by higher proline content, which explained their tolerance to drought stress. Sajedi et al. (2012) reported similar findings when they measured proline and two enzymes (P5C reductase and P5C synthetase) involved in the proline biosynthetic pathway when they screened two safflower varieties, one drought tolerant (cv. A1) and one sensitive (cv. Nira). The drought-tolerant variety was characterized by higher proline concentration which was attributed mostly to increased activity of P5C synthetase.

3.1.3 Antioxidant defense

When plants experience water deficit conditions, ROS are produced to exceed the management capacity (Gill and Tuteja 2010; Hasanuzzaman et al. 2012). As a result, ROS interact with various cellular molecules (lipids, nucleic acids, proteins) and cause irreversible damage to cells. High concentrations of ROS in plant cells such as superoxide anion radicals, hydrogen peroxide, and hydroxyl radicals lead to oxidation of lipids, proteins, damages in nucleic acids, inhibition of enzymes, and ultimately cell death (Sharma and Dubey 2005). The balance between ROS and the antioxidative defense system determines the plant survival (Selote and Khanna-Chopra 2006, 2010). Antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), and glutathione peroxidase (GPX) and non-enzyme antioxidants, such as ascorbic acid and reduced glutathione take action in order to limit the deleterious effects of ROS (Hasanuzzaman et al. 2012). In particular, SOD constitutes the end product of peroxidation of membrane lipids and is the first line of defense against ROS.

Several studies have been conducted on biochemical characteristics related to antioxidant systems in safflower cultivars under water deficit conditions (Amini et al. 2013; Hojati et al. 2011; Sajedi et al. 2012). Drought stress increased the activity of CAT, SOD, and GPX enzymes in four screened safflower genotypes (Sajedi et al. 2012). However, one cultivar demonstrated higher production of antioxidant enzymes among the rest safflower cultivars. Such biochemical characteristics could be taken as indices for drought tolerance in plants. Hojati et al. (2011) examined the capacity of two safflower cultivars to withstand water deficit conditions through activation of antioxidant systems. Antioxidant compounds such as ascorbic acid, α-tocopherol, GSH, SOD, CAT, and POX

increased under drought stress. Amini et al. (2013) also reported positive and significant correlations between antioxidant enzyme activities (CAT, APX, and POX) and seed yield for 64 safflower genotypes subjected to water stress. A significant variation was also observed for six safflower cultivars which, under moisture stress conditions, increased activities of CAT, APX, and glutathione reductase enzymes were measured, indicating the importance of these mechanisms for drought tolerance in safflower plants (Javed et al. 2013b).

3.1.4 Phytohormones

Phytohormones play a key role in plant tolerance under water scarcity (Farooq et al. 2009). Drought causes a decrease in gibberellins and cytokinin and auxin content, whereas abscisic acid (ABA) and ethylene concentrations increase. Evaluation studies on biochemical characteristics of safflower cultivars suffering from water-deficit stress have focused so far on ABA content from phytohormone point of view. ABA is produced in chloroplast or other plastids through mevalonic acid pathway from zeaxanthin. ABA is involved in many developmental processes and cell responses to abiotic stresses like drought (Weiner et al. 2010). One of the functional roles of ABA is to regulate water balance and osmotic stress tolerance, resulting in stomata closure under stressful conditions. Moreover, ABA influences positively the ion influx across root cell membrane and contributes in active osmotic solutes accumulation adjusting osmoregulation (Nayyar et al. 2005). ABA is accumulated under drought stress and gets degraded when the impact of the stress fades. It can also be produced in roots and later transported to shoots to regulate stomatal movements and leaf expansion. Sajedi et al. (2012) reported a significant increase in the levels of ABA which in combination with increased antioxidant enzyme activity and proline content, improved the drought tolerance of four safflower genotypes. Although, drought stress and cultivar did not affect ABA content; however, under stressed conditions, intraspecific variation was observed among safflower cultivars. ABA activation provokes stomatal closure, hence, a decreased CO_2 exchange rate, which in turn causes an increase in temperature (Canavar 2013). The lower the leaf water potential is, the more the aforementioned activities. Leaf temperature of safflower plants increased under drought stress, compared to well-watered plants, and this observation was attributed to the increased ABA synthesis.

3.2 Salinity

The salt tolerance of safflower is associated with inclusion of Na^+ and cytoplasmic avoidance. Salt tolerance in glycophytes is associated with the ability to limit uptake and/or transport of saline ions from root zone to shoot (Greenway and Munns 1980). Patil (2012) found that Na^+ content was more in the roots than in the stem and leaves at all salinity levels indicating that roots have the capacity to sequester high levels of Na^+ in *C. tinctorius* var. Bhima roots. In the shoots of salt-sensitive plants, accumulation of Na^+ ions within hours reduced the growth (Munns 2002; Munns et al. 2000). Sodium is toxic to many organisms, except for halo-tolerant organisms like halo-bacteria and halophytes, which possess specific mechanisms that keep intracellular sodium concentrations low. Accumulation of sodium in the cytoplasm is prevented by restricting its uptake across the plasma membrane and by promoting its extrusion or sequestration in halophytes (Hasegawa et al. 2000). High salt concentrations (>400 mM) inhibit the activities of most enzymes because of perturbation of the hydrophobic-electrostatic balance between the forces maintaining protein structure. However, toxic effects on cells occur at much lower salt concentrations (about 100 mM), pointing to specific salt toxicity targets (Serrano 1996).

3.2.1 Osmoregulation and osmoprotection

Osmotic adjustment or osmoregulation is the key adaptation of plants at the cellular level to minimize the effects of salinity-induced drought stress, especially during the first phase of salt stress (Greenway and Munns 1980; Anamul Hoque et al. 2007), and this phenomenon is considered as an important component of salinity tolerance mechanisms in plants (Neocleous and Vasilakakis 2007). It involves the accumulation of a range of osmotically active molecules/ions including soluble sugars, sugar alcohols, proline, glycine betaine, organic acids, calcium, potassium, trehalose, and chloride ions (Fig. 4). Generally, they protect plants from different environmental stresses through maintaining the osmotic balance, ROS, and stabilizing membranes and proteins (Hasegawa et al. 2000). The leaf osmotic potential was decreased with simultaneous increase in the uptake of Na^+ and Cl^- and increase in the accumulation of proline and sucrose with increase in NaCl for all tested genotypes (Matsumura et al. 1998). Major contributions to decrease leaf osmotic potential by osmoregulation under NaCl stress were the accumulations of the compatible solutes (sucrose, proline, and glycine betaine) in safflower. Salt-tolerant accessions of *C. tinctorius* (260622 and 305167) accumulated significantly greater Na^+ in leaves compared to salt-sensitive accessions (199952 and 170274) (Ashraf and Fatima 1995). In Table 2, a selected list of safflower accessions with salt tolerance potential has been elaborated. By means of osmotic adjustment, the organelles and cytoplasmic activities take place at about a normal pace and help the plants to perform better in terms of growth and photosynthesis and assimilate partitioning to grain filling (Ludlow and Muchow 1990; Subbarao et al. 2000). In fact, the degree of osmotic adjustment could be affected by the rate of stress development (Shangguan et al. 1999) and most particularly by the organ type and age (Kameli and Lösel 1995).

Table 2 Some salt-resistant accessions of safflower

Accession numbers		Country of origin	Accession numbers		Country of origin
BJ[a]	PI[b]		BJ	PI	
1239	253	Afghanistan	1855	307	India
1336	268	Afghanistan	217	–	Korea
2258		Albania	1080	250	Iran
109	Gao Qing	China	1082	250	Iran
199	Tong hua (Ji Li)	China	1111	250	Iran
2173	–	China	1112	250	Iran
2245	Wo Yang (An Hui)	China	1118	250	Iran
2254	–	China	1119	250	Iran
2255	–	China	1132	251	Iran
2594	269	China	1250	255	Iran
2685	250	China	1463	304	Iran
1072	250	Egypt	1476	304	Iran
1604	306	Egypt	1478	304	Iran
1611	306	Egypt	2074	405	Iran
2694	250	Egypt	2102	406	Iran
798	226	Ethiopia	2494	250	Iran
2213	*C. lanatus*	Germany	2496	250	Iran
698	199	India	2695	250	Iran
747	199	India	1212	253	Iraq
791	212	India	1618	306	Israel
918	248	India	1274	259	Pakistan
934	248	India	1275	259	Pakistan
936	248	India	1265	258	Portugal
962	248	India	774	209	Romania
1062	250	India	1923	314	Russia
1243	254	India	788	210	Turkey
1288	260	India	805	237	Turkey
1351	279	India	1135	251	Turkey
1390	283	India	1138	251	Turkey
1514	305	India	1139	251	Turkey
1518	305	India	1140	251	Turkey
1679	306	India	1936	340	Turkey
1708	306	India	2139	407	Turkey
1732	306	India	2634	340	Turkey
1775	306	India	–	2	USA
1820	307	India			

Source: Dajue (1993)

[a] Beijing accession numbers

[b] Plant introduction numbers from USDA

3.2.2 Sugars

Several physiological studies suggested that under stress conditions, non-structural carbohydrates (sucrose, hexoses, and sugar alcohols) accumulate although to varying degrees in different plant species (Streeter et al. 2001; Taji et al. 2002). Under salt stress, germination and relative water contents decreased that lead to reduce the proline, total soluble sugars, and activities of the main enzymes involved in the germination process (Jabeen and Ahmad 2013). However, seeds of NuSun and Spiny cultivars accumulated higher proline and total soluble sugar concentrations in response to salt stress, which improved their water status and the enzyme activities involved in the process of germination. Major contributions to

decrease leaf osmotic potential by osmoregulation under NaCl stress were the accumulation of compatible solutes (sucrose, proline, and glycine betaine) in safflower (Matsumura et al. 1998). Accumulation of these and other organic ions increased osmotic activity, causing a reduction in water potential and an inward diffusion of water from the surrounding cells which result in expansion and maintenance of cell turgor.

3.2.3 Proline

Osmotic adjustment is accomplished with the accumulation of compatible cytosolutes like proline. Proline accumulation normally occurs in the cytosol where it contributes substantially to the cytoplasmic osmotic adjustment (Ketchum et al. 1991). It is osmotically very active and contributes to membrane stability and mitigates the effect of NaCl on cell membrane disruption (Mansour 1998). Even at supra-optimal levels, proline does not suppress enzyme activity. The proline may act as a signaling/regulatory molecule able to activate multiple responses that are component of the adaptation process (Maggio et al. 2002). Proline accumulation can occur via two biosynthetic pathways in plants: the ornithine-dependent pathway and the glutamate-dependent pathway. The accumulation of Na^+ ions and osmolytes could play an important role in osmotic adjustment in safflower cells under saline stress. Generally, proline protects the plants from stress through different means such as contribution toward osmotic adjustment, detoxification of ROS, and stabilization of membranes and native structures of enzymes and proteins (Fig. 5). The proline contents were increased under salt stress, and safflower "Cyprus" cultivar had greater proline content than all other cultivars (Hosseini et al. 2010). Moreover, the salinity and drought stresses increase the accumulation of proline in safflower cultivars (PI-251978, PI-170274, PI-387821, PI-386174, and THORI-78) whereas the proline accumulation did not appear to be an essential part of the protection mechanism against salinity and drought in variety PI-387820 (Javed et al. 2013b). Malondialdehyde and free proline contents in the leaves of safflower cultivars increased gradually in proportion to the increase of NaCl concentration (ErdaL and Çakirlar 2014).

Salt resistance is a complex trait which involves the coordinated action of many genes that perform a variety of functions, such as ion sequestration, metabolic adjustment, osmotic adjustment, and antioxidative defense. The salinity decreased germination percentage, germination rate, length and weight of root and shoot, and protein content while proline content, malondialdehyde content (MDA), catalase, and peroxidase activity increased at 10.8 dS m^{-1} (Jabeen and Ahmad 2013). Salt stress enhanced leaf and root Na^+ and Cl^- ratios, proline accumulation, and activities of leaf superoxide dismutase, catalase, and peroxidase, while it decreased K^+/Ca^{2+} and Ca^{2+}/Na^+ ratios and seed yield, 100-seed weight, number of seeds and seed oil contents (Siddiqi et al. 2011). The role of proline during osmotic stress has also been proved through transgenic approaches.

3.2.4 Glycine betaine

The crops have developed strategies to mitigate the deleterious effects of salinity through the production of antioxidant enzymes like glycine betaine (GB) (Tavallali et al. 2010). This system allows plants to grow under salinity conditions by holding ROS to a minimum range (Masood et al. 2006). The hydrogen peroxide produced by salinity stress can be scavenged by peroxidase enzyme (Dionisio-Sese and Tobita 1998). The ability of compatible solutes, and GB in particular, to regulate net fluxes of Na^+ and K^+ across the plasma membrane has been reported at the cellular level, both in response to NaCl (Fig. 5; Cuin and Shabala 2007a) and ROS (Cuin and Shabala 2007b). GB is abundant mainly in the chloroplast where it plays a vital role in adjustment and protection of thylakoid membrane, thereby maintaining photosynthetic efficiency (Genard et al. 1991). Plants synthesize glycine betaine via a two-step oxidation of choline: choline → betaine aldehyde → glycine betaine (Rhoades et al. 1989). GB may serve as an osmoprotective to prevent cell damage from dehydration (Chen et al. 2001). It has been reported that GB prevents NaCl-induced K^+ leak (Cuin and Shabala 2007b) and, thus, indirectly aids water retention in plant tissues. Safflower variety, Sina 411, has proved to be salt tolerant due to having more proline and GB and higher soluble sugar contents than all other cultivars (Javadipour et al. 2013).

3.2.5 Ion homeostasis

Another strategy for achieving greater tolerance is to help plants to re-establish homeostasis in stressful environments. Various ion transporters are the terminal determinants of ionic homeostasis. Because Na^+ inhibits many enzymes, it is necessary to prevent Na^+ accumulation to a high level in cytoplasm and other organelles other than the vacuole. Any Na^+ entering into cells may be stored in the vacuole or exported out of the cell. Na^+ compartmentation is an economical means of preventing Na^+ toxicity in the cytosol because the Na^+ may be used as an osmolyte in the vacuole to help to achieve osmotic balance. Many salt-tolerant plants (halophytes) rely on this strategy (Zhu 2001). Harrathi et al. (2012) in a hydroponically grown safflower plants found that salt treatment increased markedly the concentrations of Na^+ in both plant parts while it reduced those of K^+ which resulted in a sharp reduction of K^+/Na^+ ratio. The Na^+ content was increased under salt stress while Ca^{2+} and K^+ content decreased significantly after treating safflower cultivar at higher salinity level, and safflower cultivar, Isfahan, proved to be tolerant than Cyprus cultivar (Hosseini et al. 2010).

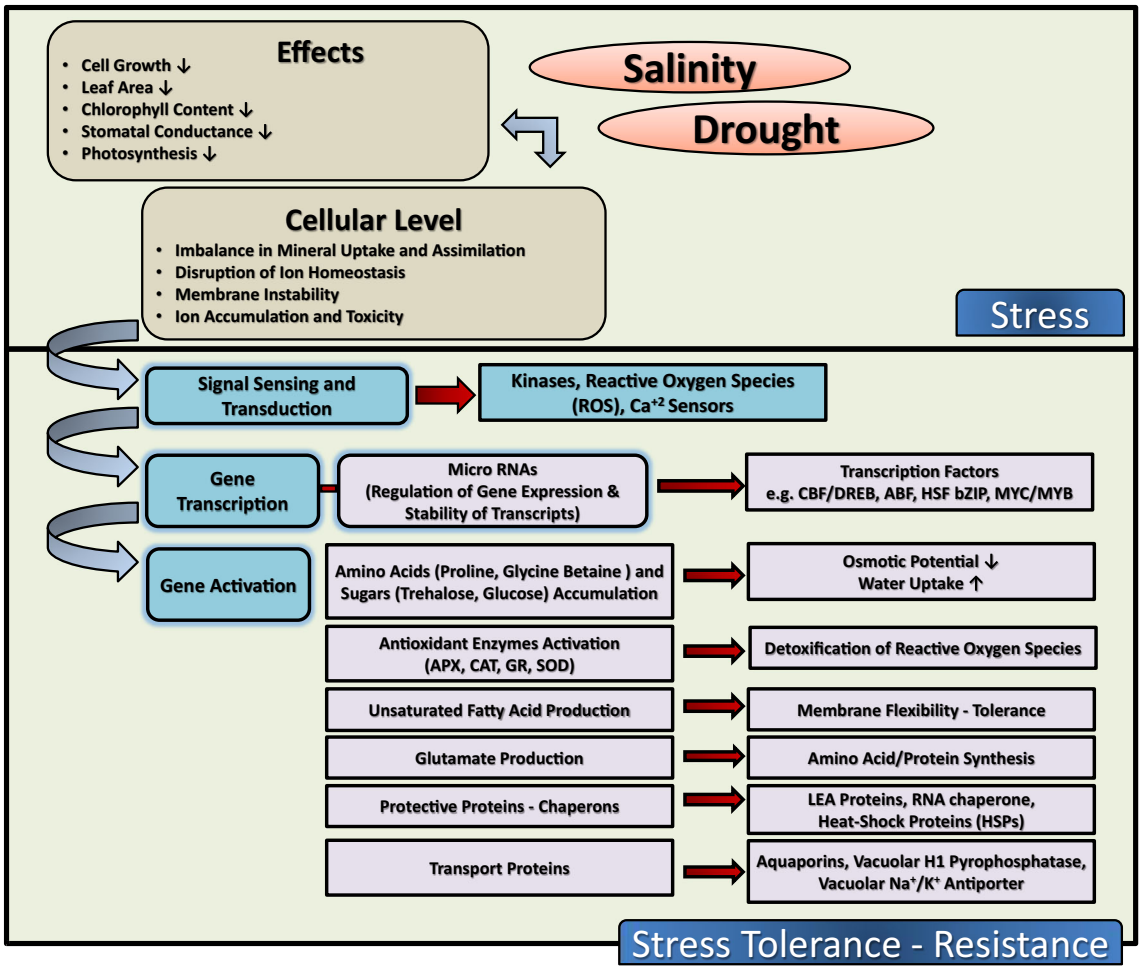

Fig. 5 Crucial stresses (drought and salinity) are frequently interrelated in safflower, causing cellular damage and secondary stresses (osmotic and oxidative). This activates the downstream signaling procedure that stimulates stress-responsive molecular mechanisms in order to invigorate cell homeostasis and restore impaired membranes and proteins

3.2.6 Antioxidant defense system

Antioxidant metabolism, including antioxidant enzymes and non-enzymatic compounds, play critical parts in detoxifying ROS induced by salinity stress. Salinity tolerance is positively correlated with the activity of antioxidant enzymes, such as SOD, CAT, GPX, APX, and GR and with the accumulation of non-enzymatic antioxidant compounds (Gupta et al. 2005; Asada 1999). Ascorbate is one of the major antioxidants present within the cell. The antioxidant glutathione helps to mitigate salt stress, which can react with superoxide radical, hydroxyl radical, and hydrogen peroxide, thereby functioning as a free radical scavenger. Javed et al. (2013b) revealed that THORI-78 safflower cultivar can tolerate salinity and drought stress through increasing CAT and APX enzyme activities whereas variety PI386174 showed increased activity of GR enzyme under salinity and drought and appeared to be very crucial antioxidative defenses during intense stress conditions. The antioxidative enzymes (catalase, peroxidase) and peroxidase activity increased in safflower cultivar (Cyprus), while Isfahan local cultivar had higher catalase activity (Hosseini et al. 2010).

3.2.7 Hormonal regulations

Application of ABA ameliorates the effect of stress condition. It has long been recognized as a hormone which is upregulated due to soil water deficit around the root. Salinity stress causes osmotic stress and water deficit, increasing the production of ABA in shoots and roots (He and Cramer 1996; Popova et al. 1995). The safflower cultivars respond differently toward salinity stress by increasing Ca^{2+} and Cl^{-} to a lesser extent while Na^{+} in their shoots and roots by decreasing the fresh/dry weight ratio (Gadallah 1996). The ratio of K^{+}/Na^{+} was decreased progressively on salinization. With stressed plants, ABA application reduced the toxicity of salt treatment, improved K^{+} uptake under salinity, effectively increased K^{+}/Na^{+} ratio, helped the plants to avoid Na^{+} toxicity, and sometimes enhanced growth. The association between the internal mineral element concentrations was largely affected by ABA

application and temperature change, but a wide fluctuation in response was noticed.

The accumulation of ABA can mitigate the inhibitory effect of salinity on photosynthesis, growth, and translocation of assimilates (Jaschke et al. 1997; Popova et al. 1995). The positive relationship between ABA accumulation and salinity tolerance has been at least partially attributed to the accumulation of K^+, Ca^{2+}, and compatible solutes, such as proline and sugars, in the vacuoles of roots, which counteract with the uptake of Na^+ and Cl^- (Chen et al. 2001; Gurmani et al. 2011). Some other compounds having hormonal properties, such as salicylic acid (SA) and brassinosteroids (BR), also participate in plant abiotic stress responses (Clouse and Sasse 1998; Fragnière et al. 2011). However, the application of SA and BR on growth, physiology, and biochemical attributes of safflower is largely unknown.

4 Management

4.1 Drought

4.1.1 Inferring safflower genetic resource diversity

Safflower (*C. tinctorius* L.) is a diploid ($2n = 2\times = 24$) oilseed crop member of the Asteraceae family. *Carthamus* derived from the Latinized synonym of the Arabic word *quartum*, or *gurtum*, referring to the flower extracted dye's color (Singh 2006). Safflower is, without a doubt, a multipurpose crop that has been cultivated for carthamin (the orange-red dye extracted from its flowers), as well as, for its rich in polyunsaturated fatty acids oil and for its medicinal properties (Dajue and Mundel 1996). Furthermore, vegetative parts of safflower can be used as pot herb and salad. In addition, safflower forage is palatable and has a great yields and feed value. Thus, each part of safflower has a value attached to it (Singh 2006). *Carthamus* has 25 species, of which only *C. tinctorius* is the cultivated type. Vavilov (1951) proposed three different areas for cultivated safflower. The first center of origin was placed in India, and it was determined based on the variability and ancient culture of safflower. A second diversity center was placed in Afghanistan, and it based on the detected proximity to wild species. Finally, the third center of origin was placed in Ethiopia due to the occurrence of wild safflower species in the region. Safflower is successfully grown under arid and semi-arid climatic conditions due to its high adaptability to low moisture conditions. As a result, its cultivation is mostly restricted to areas with limited rainfall and temperate-drought conditions in various agricultural production systems in Asia, Europe, Australia, and America (Singh 2006). Despite the fact that safflower has tremendous prospective under diverse environments and can be exploited for a range of purposes, still, safflower is a minor crop due to the lack of information on its crop management and product development from it.

Advancement in plant breeding necessitates a high genetic diversity which allows conduction of more effective selection programs. Plasticity, genetic differentiation, and selection for traits related to drought tolerance are characterized by high variation depending on climatic conditions and species (Franks 2011). Breeders seek into wild and domesticated germplasm within species to examine the genetic and adaptive diversity to drought (Berger et al. 2012a). Australian breeders have selected lupine ecotypes to escape drought by producing temperature-responsive and early phenology cultivars (Berger et al. 2012b). Several studies conducted in different regions worldwide related to screening of wild and cultivated safflower species have been focused on the identification of germplasm with drought-tolerant genes, shorter biological cycle, and early flowering to escape or confront drought (Kisha and Johnson 2012; Majidi et al. 2011; Pourdad and Mohammadi 2008; Rameshknia et al. 2013; Salamati et al. 2011; Tahmasebpour 2011; Zareie et al. 2013). Although drought adversely diminishes growth and productivity of safflower plants, high intra-specific variability has been also observed in the antioxidant enzyme production among safflower cultivars (Sajedi et al. 2012; Javed et al. 2013a). Safflower genotypes that produce higher levels of these enzymes should be selected for further breeding. Increase in activities of antioxidant enzymes was measured for safflower genotypes affected by water deficit stress, and in some cases, they were positively and highly correlated with seed yield, indicating the preponderance of some safflower accessions that could be further improved (Amini et al. 2013; Javed et al. 2013a; Sajedi et al. 2012).

Most of the genetic variation in restricted varieties and landraces of the *Carthamus* species has been eroded. Studies on the genetic diversity of safflower accessions will consequently assist to make available important information needed for the conservation and enhancement of the safflower germplasm. Recently, there is a raising interest in characterizing and exploiting its vast genetic diversity that can be further linked to desirable traits such as drought tolerance via molecular markers. Molecular markers have been used principally for the assessment of germplasm variability of local varieties, landraces, natural populations, and accessions in order to screen genetic diversity geographically (Amini et al. 2008; Johnson et al. 2007; Khan et al. 2009; Sehgal and Raina 2005; Yang et al. 2007). Since there is still inadequate genetic information, most of the markers did not require prior sequence information. Hence, application of different molecular markers such as RAPD (Amini et al. 2008; Mahasi et al. 2009; Sehgal and Raina 2005; Vilatersana et al. 2005), ISSR (Ash et al. 2003; Golkar et al. 2011; Panahi et al. 2013; Sabzalian et al. 2009; Yang et al. 2007), AFLP (Johnson et al. 2007; Sehgal and Raina 2005; Sehgal et al. 2009), and SRAP

(Mokhtari et al. 2013; Peng et al. 2008; Talebi et al. 2012) has been successfully used in identifying genetic variety but had little to contribute for the identification of characteristics linked to drought tolerance. This may be the 'default' disadvantage of these marker systems since they 'scan' the genome arbitrary. For that reason, it has been reported that detected genetic diversity within cultivated accessions is limited for a number of important characters, such as drought tolerance (Majidi et al. 2011).

However, new emerging techniques, like the expressed sequence tag-simple sequence repeat (EST-SSR) functional markers, may provide the necessary link between genetic diversity and traits of drought tolerance. As a result, recently, there are a few reports about the use of EST-SSR in molecular analyses and mapping (Barati and Arzani 2012; Chapman et al. 2009, 2010; Naresh et al. 2009). Even though EST-SSR may detect a lesser amount of diversity than genomic SSR, still the exploitation of drought-induced transcriptomic data is a very promising milestone in identifying drought-tolerant genetic recourses of safflower. Especially if such functional markers (SNPs included) are implemented to wild safflower relatives who possess a number of valuable resistance genes to stress conditions (Mayerhofer et al. 2010).

4.1.2 Evaluation, breeding, and selection

Safflower is normally a rainfed crop, but it can sustain damages owed to moisture stress. Studies regarding to abiotic stresses, such as drought, and the genetic background of drought tolerance are largely lacking in safflower (Singh 2006). Introduction is the simplest breeding method of crop improvement and has been used comprehensively. In general, the direct introduction of varieties in a new region is not common since introduced varieties necessitate a few cycles of environmental acclimation, followed by selection and evaluation of populations. As a result, selection should mainly focus on safflower germplasm that has high yielding properties. Intra-specific variability among different safflower cultivars was also reported for vegetative, flowering, and yield formation stages (Tahmasebpour 2011). The study of safflower genotypes by means of yield components (oil content, number, and seed yield) under stress conditions has been very useful in order to identify drought-tolerant, drought-resistant, and susceptible-to-water-stress genotypes. Furthermore, selection is the most frequently used breeding scheme pursued for development of varieties as far as safflower improvement. However, so far, the main breeding attempts are restricted to the evaluation of genotypes, employing different levels of irrigation or rainfall (Alizadeh 2005; Bagheri and Sam-Daliri 2011; Behnam et al. 2011; Golparvar 2011; Hasanshahi et al. 2013; Rameshknia et al. 2013; Zareie et al. 2013).

Evaluation of safflower germplasm for drought tolerance at initial growth stages showed that considerable genetic variation existed among some safflower cultivars to tolerate water stress and could offer a distinct advantage for its cultivation in dry climates. Bassiri et al. (1977) performed comparisons between cultivated safflower varieties and wild ecotypes (*Carthamus oxyacantha* Bieb.) for their tolerance under simulated moisture stress conditions. Additionally, there are even fewer studies attempting to find a link among drought tolerance and physiological mechanisms. Under rainfed conditions, among 12 safflower lines, genotypes having higher yield also had higher proline and chlorophyll contents (Mohankumar et al. 2010). Photosynthetic pigments along with other biochemical properties could be considered as useful indicators to improve safflower germplasm for drought tolerance (Amini et al. 2013). It was revealed that nitrate reductase (NRA) and nitrite reductase (NiRA) activities, and protein and DNA content are useful biochemical indicators for drought stress tolerance (Javed et al. 2013a). Furthermore, Nikzad et al. (2013) used relative water content, stomata density, and length as physiological indicators for 15 drought-stressed safflower genotypes and determined a significant decrease in the relative water content and stomatal density in drought-sensitive genotypes.

Another breeding method, alternative to selection, is hybridization which is practiced mostly to combine desirable traits of two or more varieties. Hybridization has proved to be of great use in unraveling the genetic makeup of different traits. Golkar et al. (2009) produced and evaluated 12 F1 hybrids originated from reciprocal crosses of four parental lines. Five antioxidant agents (APX, GR, SOD, LP, and carotenoid levels) were assessed under limited water availability, and it was determined that the majority of F1 hybrids had greater activity of antioxidants when compared to their parents. Golkar et al. (2012) produced 56 F1 hybrids from eight safflower genotypes and evaluated them under water stress conditions.

The presence of genetic male sterility (GMS) and cytoplasmic male sterility (CMS) systems in safflower is yet another breeding path that can produce drought-tolerant genotypes (Singh 2006). Moreover, mutation breeding is yet another promising technique for the enhancement of safflower germplasm. Mozaffari and Asadi (2006) selected drought-tolerant genotypes from the M5 generation of the gamma-rayed Zarghan 279 variety, while Akbar and Kamran (2006) evaluated, under normal and drought conditions, 13 safflower gamma-ray mutants alongside to their parental varieties. Finally, there is an increasing interest in exploiting wild safflower genetic resources since the detection and introgression of genes from wild plant species enhance the genetic improvement of plants cultivated in arid environments (Majidi et al. 2011). Their study involved the collection and evaluation of *Carthamus oxyacanthus* and established that the wild plants sustained more moisture stress tolerance than cultivated species; hence, high drought tolerance makes wild

C. oxyacanthus safflower a suitable future candidate resource for introgression of drought-tolerant traits to cultivated species. Eslam et al. (2010) studied seed and oil yields, their components, and the relationships among yield and related traits in five spring safflower genotypes under non-stressed and water deficit conditions imposed from late flowering (80 % flowering) to maturity. Their results showed significant decrease in the number of seeds per capitulum, 1000-seed weight, harvest index, and seed and oil yields under water deficit conditions and showed that these may be the most important characteristic for selecting spring safflower genotypes under drought conditions. In another study, Omidi Tabrizi (2010) evaluated safflower genotypes under three different environmental conditions in Iran and indicated significant differences among genotypes in seed and oil yields. Zareie et al. (2013) evaluated ten Iranian safflower genotypes in separate experiments under well-watered irrigation and water deficit stress at flowering stage in three growing seasons. The results of their combined analysis over the experiments showed significant variations among the genotypes for all the studied traits, and they decreased due to water stress. Moreover, they concluded flowering stage as the most sensitive stage to water deficit that in turn reduces seed yield.

Screening of safflower wild genotypes and landraces that demonstrate high productivity under drought conditions is necessary so that improved plant material through breeding systems could be cultivated in arid environments (Kisha and Johnson 2012; Majidi et al. 2011; Salamati et al. 2011; Zareie et al. 2013). A schematic representation of drought and salt stress mechanism and management has been elaborated in Fig. 5. Significant intra-specific variation for drought has been observed on morphological and physiological basis for safflower germplasm (Majidi et al. 2011; Pourdad and Mohammadi 2008; Rameshknia et al. 2013; Tahmasebpour 2011).

4.1.3 Gene mapping and QTLs for drought tolerance

Safflower molecular breeding, mapping, and quantitative trait locus (QTL) identification is largely lagging behind other oilseed crops (Hamdan et al. 2011). One reason is the limited genetic information about this species, and as a consequence, the nature of molecular markers developed for safflower (the majority of which are random amplified polymorphic DNA (RAPD), restriction fragment length polymorphisms (RFLPs), amplified fragment length polymorphisms (AFLPs), and simple sequence repeats (SSRs) which are generally dominant and unlinked). Only a few molecular markers have been correlated to quantitative or qualitative traits (Hamdan et al. 2008). Thus, genetic improvement of safflower through marker-assisted breeding and genetic linkage of traits has been very limited.

García-Moreno et al. (2011) and Hamdan et al. (2012) were able to construct genetic linkage maps for the Tph2 gene and the Ol locus, respectively, using two F2 mapping populations. Tang et al. (2010) performed a cDNA-AFLP linkage analysis using 192 randomly F2 segregating populations, in order to map heat shock protein (HSP) genes. Recently, a number of research groups have developed EST-SSR and genomic SSR markers (Chapman et al. 2009; Hamdan et al. 2011; Naresh et al. 2009) that can aid as a valuable tool for molecular breeding, mapping, and linkage of desirable QTL traits, such as drought tolerance. In particular, Mayerhofer et al. (2010) were able to produce 1412 PCR-based markers and 75 RFLP markers in order to map an intra-specific F2 population of *C. tinctorius* and an inter-specific BC1 population of *C. tinctorius* × *C. oxyacanthus*, while the two maps represented the first major linkage analysis of *Carthamus* species.

In addition, Heesacker et al. (2008) developed 16,643 EST-SSR markers from common sunflower EST libraries and inquired their transferability to closely and distantly related species of the Compositae family. Even though a low presence of these markers were common to safflower, still, their contribution to dense linkage mapping and drought-tolerant QTLs identification may be beneficial. García-Moreno et al. (2010) determined the feasibility of transferring non-genic microsatellite (SSR) markers and gene-based markers, including intron fragment length polymorphism (IFLP) and resistance gene candidates (RGC)-based markers from sunflower (*Helianthus annuus* L.) to safflower.

4.1.4 Functional genomics for drought tolerance

Abiotic stress tolerance is one of the main factors limiting safflower growth and survival. Hence, the increase of environmental stress tolerance is one of the most important goals of safflower breeding programs. Amini et al. (2013) studied 64 safflower genotypes and documented that drought-tolerant genotypes have a significant increase in antioxidant compounds (APX and POX). However, there is a research shift from the static aspects of the gene information to genome-wide studies via the utilization of high-throughput methods (opposed to the conventional 'gene-by-gene' approaches). Functional genomics are therefore likely to facilitate or even boost studies regarding tolerance of safflower cultivars to abiotic stress, such as drought.

The immense progress in sequencing techniques can provide numerous data extracted from drought-tolerant safflower genotypes or relative species. For instance, Thippeswamy et al. (2013) differentially evaluated two safflower cultivars (A1 and Nira) and identified cultivar A1 as relatively drought tolerant. In order to recognize drought-responsive genes, they constructed a subtracted cDNA library from cultivar A1 and identified 667 unique drought-responsive ESTs. Remarkably, even though that majority of them had significant homology

to other plants, more than 20 % of drought-induced ESTs were not homologous to any sequences in databases and were considered novel drought-responsive genes of safflower. Insight into the function of these genes and demonstration of their novelty may pilot to a better perception of the drought tolerance mechanisms in safflower and potentially other oilseed crops (Thippeswamy et al. 2013). Lulin et al. (2012) also conducted large-scale genomics, in order to investigate genes and pathways that may regulate flavonoids, the biosynthesis of unsaturated fatty acids (that can be beneficial to oxidative stress caused by abiotic stresses like drought), and other secondary metabolites in the safflower. Furthermore, these genes were moderately conserved in the safflower genome when compared to those of other plants. Catalano et al. (2012) analyzed 36,323 ESTs from artichoke and 42,011 ESTs from safflower and detected that 75 % of all ESTs had at least a common homologous region (*E* value $<10^{-4}$) and about 50 % of these displayed 400 bp or longer aligned sequences as conserved homologous/orthologous (COS) regions. Furthermore, they were able to identify several conserved putative microRNAs among these species. MicroRNAs can regulate gene expression or stability of transcripts and therefore exploitation of ESTs for their detection can be of immense importance for the identification and for deciphering the mechanisms of drought-related genes.

Furthermore, Cao et al. (2013) investigated the molecular basis of the high oleic (HO) trait in safflower and compared the miRNA populations in developing safflower seeds expressing the *ol*allele in comparison to the wild-type high linoleic (HL). They detected 55 known miRNAs and identified two novel miRNA families of developing safflower seeds. The results can act as a basis for unraveling the miRNA-mediated molecular processes that control gene expression of safflower at a post-transcriptional level. Finally, Li et al. (2011) reported 236 known miRNAs, of which 100 miRNAs exhibited evolutionary conservation across multiple plants. Furthermore, experimental validation of plant miRNAs showed that miRNAs expression varied upon cold, drought, and other stress responses (Song et al. 2010; Sunkar and Zhu 2004; Zhang et al. 2009), indicating that miRNAs possibly have a dynamic regulation role in plants. Hence, a comprehensive study of miRNAs in the safflower could provide supplementary evidence in order to elucidate their physiological functions and evolutionary roles in plants and stress responses (Li et al. 2011).

4.1.5 Transgenic approaches

Genetic engineering has a major part in current plant biotechnology. The essential principle of genetic modification is to enhance the genetic markup by usually integrating foreign DNA in the plant genome. Unfortunately, even though several studies exist on the routinely successful transformation of crop plants, a lot remain to be solved in crops like safflower. In some cases, genetic modification in plants can occur by direct gene transfer or vector-mediated gene transfer methods. However, in safflower, genetic engineering until now is confined to vector-mediated (*Agrobacterium*-mediated) transformation via callus-mediated regeneration (Orlikowska et al. 1995; Sankara Rao and Rohini 1999) or embryo transformation (Rohini and Sankara Rao 2000). Belide et al. (2011) developed a new protocol for transformation with significant improvements in both the efficiency (about 5 %) and simplicity of implementation over existing safflower transformation protocols. Certainly, safflower is a complex crop to genetically engineer, and many studies describe a series of limitations (Orlikowska et al. 1995; Sankara Rao and Rohini 1999) like the lack of genotype-dependent regeneration system, the low efficiency of transformation, the hyper-hydration and necrosis of *Agrobacterium*-infected cotyledons, the growth retardation of shoots, and the poor rooting and low survival following acclimatization of selected shoots.

There has been an approximately exponential increase in publications on genetic modification for drought resistance (Lawlor 2013), and therefore, the guideline for the achievement of drought-tolerant safflower genotypes has been set. At any case, as reported by Lawlor (2013), the genetic engineering of safflower for drought tolerance should aim at (i) modifications to decrease cell osmotic potential (ROS via over production of mannitol, proline, and GB), (ii) amino acid metabolism affecting protein synthesis (via production of glutamate), (iii) signaling molecules which alter the balance of cell metabolism (trehalosee, phosphatidylinositol, ononitol), (iv) protective proteins which accumulate in water-deficient cells and are considered to stabilize protein structure, act as chaperones, etc. (molecular chaperones, LEA proteins, RNA chaperone, cold-shock protein), (v) proteins involved in cell growth and metabolism (mitochondrial uncoupling protein), (vi) transport proteins of diverse functions (aquaporins, vacuolar H1 pyrophosphatase, vacuolar Na^+/K^+ antiporter), (vii) regulation of gene expression and protein synthesis (transcription factors), (viii) phytohormones and related metabolism (abscisic acid, cytokinins, farnesyl transferase, isopentenyl transferase), and (ix) energy regulation and signaling (ascorbate peroxidase, PAP, PARP, poly (ADPribose) polymerase glycohydrolase, dihydroorotate dehydrogenase).

4.2 Salinity

Development of salt-tolerant genotypes and site-specific production technology may help to sustain safflower productivity in salt-affected areas. Recent progress in the field of genomics and biotechnology, and conventional breeding approaches, has the potential to introduce transgenic safflower cultivars to perform well under salt stress. Moreover, exogenous application of certain osmoprotectants and growth regulators,

nutrient management, and seed priming techniques may also be helpful for profitable safflower production in saline areas.

4.2.1 Selection and breeding approaches

Mass screening of safflower genotypes is often used to identify salt-tolerant germplasm for breeding programs and to develop better-performing genotypes for salt-prone areas. Quick screening for salt resistance, on the basis of some agronomic traits, during early growth stages of safflower is often deemed valuable. Conventional breeding involves development of a breeding population highly variable for desired traits followed by combining the target traits to develop genotypes better able to perform well in a specific environment.

Although several screening and selection criteria are being used; however, screening for salinity tolerance is more operative if that is done using the physiological traits (Flowers and Yeo 1995; Shannon and Noble 1990), especially in safflower. In another study, Siddiqi et al. (2009) screened safflower genotypes for salinity tolerance (150 mM NaCl at the vegetative stage), and plant total biomass and photosynthetic attributes can be used as selection criteria for salinity tolerance. Taffouo et al. (2009) also supported to use photosynthetic attributes as key indicator of growth regulation in plants under salt stress. However, Nikbakht et al. (2010) suggested to use certain other indices like stress susceptibility index, geometric mean productivity tolerance index, and stress tolerance index (STI) as selection criterion for developing salt-tolerant safflower genotypes. Nonetheless, the traits taken as selection criteria should be easy to measure, correlated with grain yield, and should be heritable.

There is wide genetic diversity in wild safflower species in terms of adaptability, oil quality, and resistance abiotic stresses including salinity. Nonetheless, introduction of acquired traits from wild *Carthamus* species is restricted due to variation in basic chromosome number, sensitivity to day and night length, and delayed flowering. However, in cultivated safflower, the reproductive isolation hurdles are less, particularly in species with $2n = 24$ chromosomal number, and thus possess great potential for improving genetic variation in cultivated *Carthamus* species. Moreover, safflowers breeding through inter- and intra-specific hybridization together with molecular characterization may help in tracking gene and successful introgression of genes in cultivated germplasm (Sujatha et al. 2008). In conclusion, mass screening for salt tolerance may be done on the basis of photosynthesis. The genotypes selected may be used in the breeding programs aimed at developing salt resistance safflower genotypes.

4.2.2 Marker-assisted selection

Marker-assisted selection is an effective approach for development of salt tolerance in safflower as visual selection procedure is time consuming and difficult. Marker-assisted selection may speed up the breeding efforts (Mantri et al. 2010; Ribaut and Ragot 2007; Wei et al. 2009). Molecular markers associated to the desirable traits are quite effective (Delannay et al. 2012), and identification of desirable loci associated with molecular markers is considered as an efficient tool in the crop improvement programs aimed at salt tolerance.

ISSRs, AFLPs, and RAPD are the most commonly used markers in safflower. As these markers are suitable for crops with insufficient genomic resource, these markers do not require any previous information and do genome scanning along with repetitive sequences. Many studies have reported safflower genetic diversity by using combination of phenotypic variation and molecular polymorphism (Amini et al. 2013; Johnson et al. 2007; Khan et al. 2009; Yang et al. 2007). However, development of genomic and molecular resources is limited in safflower as compared to other members of Asteraceae family, and commonly, SSR, RAPD, and AFLP markers are used for evaluation of landraces, germplasm, and genetic diversity and also to assess the outcrossing of safflower with weedy relatives (Sujatha et al. 2008). Identification of genomic regions associated with salt tolerance and its components under salt stress will be useful for marker-based approaches to develop salt-tolerant safflower genotypes. Although marker-assisted selection has the potential to develop better salt-tolerant safflower genotypes; nonetheless, selection of suitable markers is a major hindrance in this technology.

4.2.3 Biotechnology and functional genomics

Transgenic approach, transferring one or more genes from one species to another to provoke desired qualitative and quantitative characters, is much faster than conventional breeding and ensures induction of desired genes without entry of surplus genes from the donor organism. Advances in functional genomics and biotechnology have made it possible to recognize salinity-responsive genes to establish plants with better salt resistance through transgenic approaches. For instance, the Na^+ exclusion from cytoplasm to the apoplast or its compartmentation in vacuoles through plasma membrane or tonoplast Na^+/H^+ antiporters is an adaptive mechanism to avoid the toxic effects of excess Na^+ ions in safflower plants. There are several success stories in this regard. For example, overexpression of (*NHX1*) genes controlling vacuolar Na^+/H^+ antiporter that store Na^+ in vacuoles improved the salinity tolerance in *Arabidopsis*, tomato, and brassica (Aharon et al. 2003).

In safflower, *Agrobacterium*-mediated transformation protocols have been reported (Rohini and Sankara Rao 2000). However, the protocols have not been exploited for development of transgenic with agronomically desirable traits.

Safflower suffers from lack of well-developed genetic resources. As of now, 285 nucleotide sequences and 41,000 ESTs are reported in safflower through subtractive genomic library and compositae data base. However, development in biotechnology and functional genomics for safflower may help to develop salt tolerance in this very important crop.

5 Management options

5.1 Planting time and geometry

Several studies conducted globally report that safflower can be cultivated either as a winter crop in regions having mild temperatures, or as spring crop in cooler areas, even though autumn sowing produces a significant increase in seed yield over that sown in spring (Golzarfar et al. 2011; Koutroubas et al. 2004; Yau 2007). As a result, planting date is vital in order to have a high yield and to successfully confront abiotic stresses like drought. Even though several reports detected that germination, rosette duration, plant height, weight and head per plant, grain filling duration, grains per head, and grain yield of safflower are heavily affected by planting date, unfortunately, sufficient data on successful safflower production management are currently missing. The crop is usually sowed in 6- to 20-in. rows, and narrow rows are preferred for weed competition and preservation of humidity because of the reduced evaporation. However, wider row spacing can decrease disease incidences; it can also promote weed advancement, lesser branching, delayed maturity, and lower oil content of seed. Therefore, recommended seeding depth is 1 to 1.5 in. at a rate of 25 to 30 kg ha^{-1}. Furthermore, it has been reported that a shallow planting depth promotes a uniform emergence that is important when planting early.

In order to determine the optimum plant density and evaluate the effect of drought stress on yield and oil content of safflower, Khoshnam et al. (2012) conducted a survey in Iran using four irrigation regimes and determined that as plant density was increased up to 40 plants per square meter, seed and oil yields were increased up to 1792 and 801 kg ha^{-1}, respectively, and then gradually decreased. Yau (2007) indicated that late seeding of spring safflower in semi-arid Mediterranean environments resulted in lower seed yield because later flowering coincided with terminal drought and heat. Furthermore, Tahmasebpour (2011) reported that the effects of drought had an uneven affect at different developmental stages of safflower. By testing six different genotypes in a complete randomized block design with three replications (normal irrigation and water deficit stress at both the stem elongation and flowering stages), they revealed that the flowering time was the most sensitive stage to water deficit. Hence, in an arid environment, an early seeding is advised. During drought conditions, Eslam et al. (2010) reported that one to three irrigation schemes can result to more than a 220 % yield increase. Esmaeili and Soleymani (2013) developed a method in order to calculate evapotranspiration in safflower cultivations based on meteorological data. Hence, considering the accuracy of the ET-HS model in arid regions, the minimum water consumption for maximum crop yield can be determined.

Seed coating can be a helpful procedure when it comes to drought conditions. The main problem in cultivating safflower in drylands and cold areas is that spring planting cannot produce the full crop potential, owed to the limited growing period and terminal drought stress (Dizaj 2010). On the contrary, during the winter sowing, a lot of plantlets die because of deep frost. Thus, it seems that seed coating can aid seed survival during winter when the conditions for germination are not optimal by delaying germination until spring when the conditions are more favorable. Furthermore, the limitations of spring-sowing and the prospective of late autumn-sowing initiated researches for delaying germination of the autumn-sown crops, particularly in cold regions where the winters are too severe for common winter crop stress. As a result, several procedures employing hydrophobic or water-resistant polymers for the production of coated seeds for delayed germination have been patented (Dizaj 2010).

5.2 Nutrient management

Nutrient management is one of the critical inputs in achieving a high productivity of safflower (Mündel et al. 1994). Nitrogen and phosphorus are the two essential nutrients for safflower growth and development; hence, optimization of their dosage can increase the seed yield and oil content in safflower. Soil tests are usually needed in order to determine whether additional nutrients are required. The amount and type of fertilizer needed for safflower cultivations depend on the yield goal, its position in the rotation, and the crop species used in rotation. Because safflower has deeper and stronger roots compared to small grains, thus, it can efficiently utilize the remaining reserves in soil from previous crops, up to a depth of 3 m. It has been shown that the use of phosphorus fertilizer in dry land farming improves seed yield and quality. Potassium fertilizer (K_2O) is mainly applied when very small amounts are present, while a soil pH of 6.0 seems to be sufficient.

Taheriasbagh et al. (2008) showed that with increased drought stress, the protein percentage increased significantly. Golzarfar et al. (2011) conducted a field study in an arid region of Iran (Qazvin) with the objective of determining the consequence of different nitrogen and phosphorus fertilizer rates on yield and yield components of safflower. Three different nitrogen and three phosphorus fertilizer rates in two planting seasons (autumn and winter) were tested. They determined that an increase of nitrogen and phosphorus rates had a

positive effect for all assessed traits for both seasons. They detected that the highest seed yield was obtained by an application of 150 kg N ha^{-1} and 100 kg P_2O_5 ha^{-1} (autumn planting).

In recent years, researchers have developed an increasing interest in using alternative biological fertilizers (vermicompost), involving the joint action of earthworms and mesophilic microorganisms (Aira et al. 2002). Vermicomposts have consistently improved seed germination, growth, and development more than the mere conversion of mineral nutrients into more plant-available forms. Taleshi et al. (2012) detected that seed yield and yield components increased with application of vermicomposts under water stress. Another aspect that could provide efficient crop yield for safflower under arid conditions could be the symbiosis with microorganisms. It has been reported that mycorrhizal fungi can increase root length and density or even the root morphology, hence enabling plants to occupy more soil volume and intake additional water than uninfected plants during drought (Davies et al. 1996; Kothari et al. 1990). Davies et al. (1993) reported that extraradical mycorrhizal hyphae may also bind soil to roots and preserve improved root-soil contact during drought and thus aiding the water uptake. Furthermore, the improved drought tolerance and recovery by mycorrhizal plants could be related to the enhanced P uptake (Fitter 1985; Graham et al. 1987; Nelsen and Safir 1982). It is well established that mycorrhizae improves root P uptake, and certainly, drought conditions can reduce P flux to the root surface (Gahoonia et al. 1994), in addition to growth of the root system (Mackay and Barber 1985).

Application of plant anti-transpirants is one of the main tools to balance leaf transpiration and water loss prevention (Goreta et al. 2007). Atrazine foliage spraying in low concentration would be useful as an anti-transpirant. Bagheri et al. (2012) studied the possibility of oil and seed yield enhancement of safflower (cv. Sina) by foliar atrazine application in three phenological stages including stemming, flowering, and seed filling at 0, 80, 120, and 160 g active ingredient (a.i.) ha^{-1} concentrations in a rainfed safflower. Applying atrazine at 80 and 120 g a.i. ha^{-1} specially in flowering stage increased significantly oil content from 30 to 35 %, photosynthesis rate, and seed and oil yield. There was no effect on oil content when atrazine was applied in stemming stage. Foliar application of atrazine of 120 g a.i. ha^{-1} could be recommendable in rainfed safflower production, but the higher dose up to 160 g a.i. ha^{-1} would be toxic and misplace ablative effect on safflower seed and oil yield. Zn and Mn nutrition can affect the susceptibility of plants to drought stress (Khan et al. 2003). Movahhedy-Dehnavy et al. (2009) studied the effect of foliar application of Zn and Mn on the growth and development of safflower under water deficit conditions. They reported small differences between the treatments, and linoleic acid and oleic acid comprised about 90 % of the fatty acid composition.

Several reports highlighted the potential of externally applied macro- and micronutrients for improving salinity tolerance of safflower (Table 3; Gorgi et al. 2010; Jabeen and Ahmad 2011). For instance, foliar application of KNO_3 reduced the uptake of Na^+ and Cl^- and increased the leaf area, dry and fresh weights of safflower plants (Jabeen and Ahmad 2011). Application of KNO_3 also improved the NO_3^-, soluble protein and nitrate reductase activity in both saline and no saline environments (Jabeen and Ahmad 2011). In a hydroponic study, inclusion of calcium under salt stress also helped in improving plant growth (Gorgi et al. 2010). Zn application has been found to ameliorate the adverse effects of salinity in safflower. Zn reduced excess uptake of Na^+ by safflower plants under saline conditions, probably by affecting the structural integrity and controlling the permeability of the root cell membrane (Gadallah and Ramadan 1997).

5.3 Seed priming

Suboptimal crop stands due to poor and erratic seed germination is a challenge for profitable crop production in saline areas. Salt stress substantially reduces and delays germination in safflower due to salinity-induced osmotic stress and toxic effects of Na^+ and Cl^- ions on germinating seeds. Seed priming is a short-term and pragmatic approach to cope with salt stress. In seed priming, seeds are partially hydrated which allow pregermination metabolic activities to occur without radicle protrusion (Farooq et al. 2006).

Seed priming with inorganic salts has been quite effective in improving the stand establishment, growth, and economical yield of safflower under salt stress. For instance, seed priming with NaCl and KCl improved the seedling establishment and growth of safflower grown under saline condition (Table 4; Elouaer and Hannachi 2012; Aymen et al. 2012). In addition to improvement in stand establishment, seed priming is also helpful in mitigating other adversities of salt stress. For example, in safflower, seed priming with NaCl ameliorated the adverse effects of salt stress by improving the proline contents, net assimilation rate, and K^+/Na^+ ratio (Rahimi et al. 2012). The benefits so gained from seed priming are translated into economic yield and related traits. In field experiments, hydro-priming of safflower (*C. tinctorius*) seed for 12 h resulted in a higher number of plants per square meter, capitula per plant, grains per capitulum, 1000-seed weight, grain yield, and

Table 3 Role of different mineral nutrients (KNO_3, $ZnSO_4$, and $KNO_3 + H_3BO_3 + Fe\text{-}EDTA$) in improving resistance against salt stress in safflower

Nutrient	Application mode	Parameter	Increase over control (%)	References
KNO_3	Foliar application	Leaf dry weight	+50	Jabeen and Ahmad (2011)
		Soluble proteins	+24	
		Nitrate reductase activity	+418	
$ZnSO_4$	Rooting medium	Root fresh weight	+28	Gadallah and Ramadan (1997)
		Root dry weight	+55	
$KNO_3 + H_3BO_3$ + Fe-EDTA	Foliar application	Shoot fresh weight	+167	Jabeen and Ahmad (2011)

oil content compared to untreated seed (Bastia et al. 1999).

Plant growth regulators and osmoprotectants are widely used to neutralize the damaging effects of salt stress on plants. The use of these substances, as seed priming agents, has the potential to ameliorate toxic effects of salt stress in safflower because of their role in detoxification of toxic substances and ROS. Salicylic acid (SA) is an important secondary metabolite that induces salinity resistance in plants by regulating several physiological processes through signaling. Seed priming with SA or salicylhydroxamic acid was quite effective in improving the stand establishment, seedling growth, and dry matter accumulation of safflower under salt stress (Echi et al. 2013). Chitosan is a linear polysaccharide composed of randomly distributed glucosamine. Seed priming with chitosan increased the activities of catalase and peroxidase in safflower under salt stress. Seed priming with low concentration of chitosan improved the germination and reduced the malondialdehyde (Jabeen and Ahmad 2012). In crux, the use of seed priming techniques may help in improving the stand establishment, growth, and economic yield of safflower under salt stress.

6 Conclusions

Salinity and drought are hindering the expansion of crop production in arid and semi-arid areas of the world. Safflower is an important industrial and multipurpose crop moderately tolerant to abiotic stresses. Osmotic imbalances, ionic toxicities, and water deficit cause delay and erratic stand establishment, disturb the cellular metabolism, growth and developmental cascades, and productivity. Mass screening, breeding, and marker-assisted selection for salinity and drought may help in developing safflower genotypes better able to yield well under these stresses. Seed priming and exogenous application of osmoprotectants to seed or growing plants may help the plants to perform well under salinity and drought. The use of functional genomics and biotechnological tools should be used in developing safflower genotypes resistant to salinity and drought.

Table 4 Role of seed priming agents (salicylic acid, potassium chloride (KCl), chitosan, and salicylhydroxamic acid) on the growth and physiological and biochemical traits in safflower under salt stress

Priming agent	Parameter	Increase/decrease over control (%)	References
Salicylic acid (50 ppm)	Shoot dry weight	+205	Moghadam and Mohammadi (2013)
	Root dry weight	+280	
KCl (5000 ppm)	Seedling fresh weight	+23	Aymen et al. (2012)
	Petal yield	+30	
	Number of heads/plant	+54	
Salicylhydroxamic acid (100 ppm)	Seedling dry weight	+134	Echi et al. (2013)
	Germination percentage	+34	
	Catalase activity	−71	
	Peroxidase activity	−79	
Chitosan (0.25 %)	Seedling dry weight	+10	Jabeen and Ahmad (2012)
	Protein contents	+425	
	Proline contents	−33	
	Malondialdehyde contents	−45	
	Catalase activity	−57	
	Peroxidase activity	−382	

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