A Review of Drought Tolerance in Safflower

ABSTRACT

Safflower (Carthamus tinctorius L.) is a multipurpose crop that can grow in arid and semi-arid environments because of its tolerance to drought stress, salinity, lower and higher temperatures. Despite safflower's drought tolerance characteristic, drought stress can negatively impact its growth and development. Drought stress reduces plant height and biomass, leaf chlorophyll content and area, photosynthesis rate, yield components, oil content and yield, and fatty acid composition of safflower. Increased root to shoot ratio and growth of the root are some of the drought adaption mechanisms of safflower. Recent studies have reported biochemical and molecular drought tolerance mechanisms of safflower, but they are still in infancy stages. Understanding these mechanisms can help in the management and breeding of cultivars with enhanced drought tolerance. This review compiles literature on the mechanisms of drought stress tolerance in safflower and approaches are proposed that can enhance better safflower management under water stress.

Comment [DK1]: ITALICS

Keywords: Antioxidants; Carthamus tinctorius L.; drought stress; tolerance mechanisms; crop management.

1. INTRODUCTION

Safflower is a multipurpose oilseed crop that is of high value due to its high-quality cooking oil composed of polyunsaturated (linoleic) and monounsaturated (oleic) fatty acids. Safflower is used for food, medicinal, industrial, animal feed, and floriculture purposes. It is a temperate zone crop that can be grown in the arid and semi-arid climates because it is cold, drought, and saline tolerant [1], [2]. Compared to other oilseed crops, safflower has remained a minor crop, it is grown in over 20 countries in an area greater than 1,000,000 ha worldwide [3]. It is the most drought tolerant oil seed crop which can produce reasonable seed yield in semi-arid climates [4]. Drought stress is one of the most significant constraints limiting crop production in the semi-arid and arid regions of the world. The recurrence, duration, and severity of drought in the future are predicted to increase because of decreased regional precipitation but increased evapotranspiration brought by global warming [5]. The dangers caused by drought stress instigated crop scientists to develop methods of alleviating drought tolerance in plants. Comprehending how plants respond to drought stress is important in identifying a crop's special growth traits that could be used in breeding for tolerance and refinement of agronomic practices. Drought tolerance in crops is controlled by multiple genes having additive effects and they interrelate with genes controlling yield potential, hence limiting improvement in drought tolerance in crops [6]. Plants have developed intricate techniques of surviving drought stress by changing their metabolic processes resulting in morphological, physiological, and biochemical changes [7]. Some of the techniques include closure of ~~stomates~~stomata, cellular adaptations, membrane integrity, carbon fixation rate, reactive species scavengers, induction of stress related genes, and enhanced accumulation of osmoprotectants, plant hormones, enzymatic antioxidants, protective proteins, and functional proteins [8], [9]. Drought stress tolerant plants naturally biosynthesize and accumulate unique metabolites which help to alleviate the effects of water stress; however, some plants lack the ability to biosynthesize these unique metabolites [8]. Thus, this review aims at compiling existing reports on the effects and response of safflower to drought and the mechanisms that safflower uses to adapt to drought stress. It also provides some management strategies for use underwater limiting conditions.

2. RAMIFICATIONS OF DROUGHT STRESS ON VEGETATIVE AND REPRODUCTIVE GROWTH, OIL CONTENT AND FATTY ACID COMPOSITION OF SAFFLOWER

2.1 Plant Height

Plant height is one of the growth variables that indicate the vegetative growth of plants. Depending on the breeding objectives, safflower genotypes with a higher plant height may be desirable because of increased probability of generation of more primary branches which may indirectly increase the seed yield due to the high number of capitula per plant. Drought stress has been reported to significantly reduce safflower plant height [10], [11], [12], [13], [14].

2.2 Plant Biomass

Many plant responses to water stress are mediated via alterations in plant water relations. Mild water stress can limit the growth of new roots and shoots, and gas exchange, even before the plant water deficit symptoms are noticeable [15]. Plants first detect water limitation in the root system [16]. Therefore, root development is critical in a plant’s ability to tolerate drought. Safflower plants develop a strong and deep tap root making them capable to endure long periods of drought in arid and semi-arid climates [6], [17]. Safflower plants grown under drought stress has been reported to have a high root to shoot ratio [18], [19]. The high root to shoot ratio under drought stress has been proposed to be the mechanism by which safflower plants absorb water from deeper soil layers, which is unavailable for most field crops with less developed root system [15]. Drought stress reduces shoot biomass, and root fresh weight and length of safflower [11], [20], [21]. Root traits have an important role in plant drought stress tolerance. In safflower, root length tends to increase more under drought stress. Increased root length in safflower plants occurs under drought ~~stress,~~stress;

however, root dry weight was significantly reduced [18]. Knowledge of root traits and how they are related to whole plant mechanisms to enhance crop productivity under water stress is needed. Root traits associated with maintaining plant performance under water stress include small fine root diameters, long roots, and high root density [22], [23], [24].

2.3 Leaf Area

Leaf area (LA) is one of the primary factors for photosynthetic activity and photosynthates accumulation. Plants with a large LA and high chlorophyll content accumulate more photosynthates and produce high biological yield [25]. Leaf area index (LAI) is a good indicator for crop growth and soil conditions for enhancing crop productivity [19]. Reduced plant size, LA, and LAI are major attributes for moderating water use and reducing injury under water deficit [26]. Water stress reduces leaf number, size, color, and vigor in many crops [9]. Thinner stems with fewer, dry, and smaller leaves in safflower drought stressed plants than unstressed plants have been observed [11]. While severe drought stress slowed leaf elongation and seized leaf growth and development in safflower [17]. Water stress is consistently reported to reduce LA of safflower [21], [26-27].

2.4 Chlorophyll content

The leaf chlorophyll content of plants is of significance in determining the photosynthetic rate and dry matter production [26]. Drought stress decreased leaf chlorophyll content of safflower [21], [26], [27], [28], [29], [30]. Though reduction in leaf chlorophyll content is a common occurrence in plants grown under limited water, it cannot be solely used to select drought tolerant genotypes, but it should be used in combination with other drought tolerance indices.

2.5 Photosynthesis

Photosynthesis is the process by which plants capture light energy and transform it into chemical energy in the form of complex organic compounds that they require as a source of energy. Abiotic stresses (drought, salinity, and unfavorable temperatures), significantly and negatively impacts on the photosynthetic rate of plants by changing the ultrastructure of the organelles, and concentration of pigments and metabolites, which prevents carbon assimilation and damages photosynthetic apparatus [31]. Stomatal closure is one of the drought avoidance mechanisms. It is one of the first steps in plant's adaptation to water deficit, allowing the water status to be maintained [32]. Hence, by adjusting stomatal opening, plants can control water loss by reducing the transpiration flux and limit the diffusion of carbon dioxide (CO_2) [16]. The decline in intercellular CO_2 following stomatal closure and the lower light use efficiency under drought stress reduces the functioning ~~of~~ in the photosynthetic machinery to match the available carbon substrate [33]. Research findings have demonstrated reduction in photosynthetic ability of safflower plants under water stress [12], [26]. Drought stress at vegetative and reproductive developmental stages of safflower plants reduced photosynthetic rate and the reduction depended on genotype [12], [26].

2.6 Relative Water Content

The measure of plant water content is referred to relative water content (RWC). A decrease in plant RWC under drought stress in safflower has been reported [18], [29], [34]. The RWC of two safflower varieties were significantly reduced due to drought and the rate of decrease depended on the severity of the drought [18]. Drought stress is further reported to significantly decrease safflower plant RWC irrespective of genotype [35]. The genotypic variation in safflower plant RWC was attributed to differences in the ability of the genotypes to absorb water [35]. Their results further demonstrated that safflower genotypes that had higher plant RWC had the lowest yield loss, longer stomata, and larger LAI than plants with lower RWC. This suggests that plant RWC could be used to screen drought tolerance among safflower genotypes.

2.7 Seed Yield

Drought stress is reported to significantly reduce safflower seed yield [6], [13], [36], [37]. The diminution of crop yield caused by drought stress is a major concern for agronomists and plant breeders because of scarce water resources to sustain crop productivity in arid and semi-arid regions of the world in the context of climate change [6], [33-34], [38]. Drought stress during the seed filling stage of safflower plants significantly decreases capitulum size, seed number per capitulum, 1000-seed weight, and seed yield [34]. Seed yield of safflower was significantly reduced by 17.2% under drought conditions compared to normal conditions [14]. However, the genotype 'Parnian' consistently had high seed yield in both normal and drought stress conditions [14]. This indicated the importance of using or breeding superior genotypes with acceptable performance under drought for the sustainability of production in view of climate change.

2.8 Oil Content and Composition

Safflower seed contains high quality oil use for cooking and in the food industry. The oil is rich in polyunsaturated (linoleic, γ-linolenic, and α-linolenic acids) and monounsaturated (oleic, palmitoleic, and eicosenoic acids) fatty acids [39]. Drought stress decreases safflower oil content, yield, and fatty acids composition [12], [14], [34], [40], [41]. Occurrence of drought stress at the vegetative, flowering, and/or seed filling stages significantly decreases safflower oil content [14], [34]. Drought stress affects the fatty acid composition of safflower oil by significantly decreasing linoleic acid, but increasing palmitic, stearic, and oleic acid contents, respectively, in all genotypes evaluated [14], [42]. The growing season also affects the fatty acid composition of safflower oil [39]. In Botswana, safflower grown in winter has significantly higher linoleic fatty acid content than summer [39]. On the contrary oleic acid (monounsaturated), and total saturated fatty acid content (stearic, palmitic, and arachidic) were lower in winter grown safflower than summer [39]. The differences in fatty acid composition due to the growing season was attributed to changes in seasonal temperature after flowering [39]. The variation in the fatty acid composition of oil crops including safflower is influenced by environmental factors temperature and humidity [43], [44], precipitation [45], and genes [46], [47]. Among these factors, temperature plays a greater role in safflower fatty acid composition [9], [39], [43], [48].

Other studies have reported increase [30] or no influence [13] of drought stress on safflower oil content. Drought stress increased safflower oil content [30]. The increase in safflower oil content due to drought stress was attributed to alteration of plant dynamics, which prioritized the partitioning and translocation of photoassimilates to the seeds in comparison to other plant parts [30]. However, no significant influence of drought stress on safflower oil content has also been reported [13].

3. DROUGHT TOLERANCE MECHANISMS

Drought stress is one of the main abiotic ~~biotic~~ factors that adversely limits growth, development, and yield of crops in arid and semi-arid climates [6], [13], [24], [36-37]. Plants have evolved defense mechanisms to adapt, cope, escape or tolerate drought stress by changing their metabolic activities, morphological, physiological, molecular, and biochemical traits [24], [37]. Climate change has made drought a significant threat to sustainability of crop and animal productivity, hence food security in the world.

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3.1 Accumulation of Osmoprotectants

Plants growing under water limiting conditions maintain the water potential below that of the soil by producing compatible organic solutes to avoid dessication [9], [49]. These organic solutes accumulate in the cytoplasm to cause the osmotic potential to decrease below that of the soil to facilitate water uptake, maintain cell membrane integrity and water potential equilibrium with the cells of drought stressed plants [50]. The major osmoprotectants are sugars, betaines, and amino acids [51]. Proline is one of the widely studied osmolyte in relation to abiotic stresses in plants. High levels of proline have been associated with heat shock proteins which assist in protection against stresses by controlling the proper folding and conformation of the cell membrane and enzymatic proteins. Proline and soluble proteins have been hypothesized to protect plants from drought stress by osmoregulation, reduced production of reactive oxygen species (ROS), and stabilize membrane integrity, structural properties of proteins and enzymes [52]. Reports in literature have demonstrated that drought stress increases proline content in safflower plants [13], [20], [28-29], [37], [53]. An increase in proline levels in drought stressed safflower cultivars was observed and the proline levels were influenced by cultivar or genotype [28]. The proline content in the roots and leaves of drought stressed safflower plants were five times higher than in non-stressed plants [53]. The accumulation of proline in plant tissues under water deficit conditions is attributed to the expression of a specific genes responsible for proline and pyrroline-5-carboxylate synthase biosynthesis [37], [54], [55] and inhibition of proline dehydrogenase. Carbohydrate sugars as osmoprotectants control the osmotic adjustment, maintain cell membrane integrity, and scavenge toxic ROS in drought stressed safflower plants [13], [29], [40]. Evidence shows a higher accumulation of reducing sugars as osmoprotectants in the leaves and roots of drought stressed safflower plants [29], [40], [53]. A large genetic variation in the accrual of osmoprotectants in drought stressed safflower plants has been reported in literature [13], [20], [28-29], [53]. This implies that genotypes which exhibit low levels of osmoprotectants could be improved by genetic engineering for increased accumulation of osmoprotectants.

3.2 Production of Enzymatic Antioxidants to Scavenge Reactive Oxygen Species

The ROS are produced in reasonable amounts in different cell compartments during normal plant growth, but the production increases due to the occurrence of stress. Drought stress increases the synthesis of ROS which can oxidize cellular components such as lipids, carbohydrates, DNA, and proteins [56], [57]. Uncontrolled oxidation of these cellular components will lead to death of cells [56-57]. Plants have complex antioxidant defensive techniques consisting of non-enzymatic and enzymatic components to scavenge ROS [56], [58]. The non-enzymatic antioxidants consist of carotenoids, tocopherols, glutathione, and ascorbate which serve as defense agents for protecting plant cells from oxidative damages [59], [60]. The main ROS scavenging techniques consist of glutathione reductase (GR), ascorbate peroxidase (APX), superoxide dismutase (SOD), peroxidases (POX), peroxiredoxin (PrxR), catalase (CAT), monodehydroascorbate reductase (MDHAR), and dehydroascorbate reductase (DHAR) [37], [56], [59], [61]. These ROS scavenging defensive apparatus are in various cell organelles with exception of CAT that is exclusively located in peroxisomes. These antioxidant enzymes reduce the uncontrolled oxidation caused by ROS [59], [62]. Research in safflower grown under limited water conditions demonstrate increased activities of SOD, CAT, APX, APX, and GR [13], [18], [20], [26], [37], [63]. Safflower genotypes with high activity of SOD, CAT, APX, POX, and GR are reported to be more drought tolerant than those low in the activity of the same enzymes [18], [26], [37], [63]. Under severe water stress, ROS are not scavenged, therefore they accumulate in plant cells becoming phytotoxic and disrupting cellular metabolism leading to damage of cells and expression of new genes [56-57], [63].

3.3 Proteins Induced by Drought Stress

Drought stress induces or represses various genes with different functions or regulatory at cellular level. The functional proteins include heat shock chaperones and late embryogenesis abundant (LEA) proteins [51]. The LEA are a complex group of proteins that are usually expressed during embryogenesis, or in vegetative tissues, in response to abscisic acid induced by biotic and abiotic stresses [51]. Studies on the response of these proteins under drought stress are still lacking in safflower. However, drought ESTs encoding LEA proteins in safflower have been identified [28] and these results may serve as a platform in further studies related to drought stress tolerance in safflower. Heat shock proteins (HSPs) are functional proteins, and they are known to show a high level of expression in stressed cells. Their accumulation is reported to confer protection against several stresses [65]. They are usually undetectable in vegetative tissues under normal growth conditions but can be induced by environmental stress and developmental stimuli [66]. Recently seven HSPs have been identified in safflower drought tolerant genotype EST [67]. All the identified HSPs were expressed in response to heat, cold, and cadmium stresses [67]. Although the HSPs are known to be upregulated under drought stress in other crops, the significance of chaperon in drought tolerance of safflower is not well understood [67]. Therefore, more studies with safflower should be undertaken to elucidate the role of HSPs and LEA proteins in combating the deleterious ramifications of abiotic stresses in arid and semi-arid regions of the world which experience extreme of temperatures, salinity, and frequent droughts, since genes encoding LEA and HSPs have been demonstrated to improve drought tolerance in genetically engineered plants [68].

The regulatory proteins play a role in the modulation of signal transduction and gene expression [69]. Transcription factors (TFs) are regulatory proteins that are critical regulators in the changes of gene expression induced by abiotic stresses [70]. There are many types of TFs that regulate plant response to abiotic stresses. Some of the TFs that have been recognized in safflower induced by drought stress are WRKY (WRKY domain binding transcription factors) [71], bZIP (basic leucine zipper), ERF (ethylene-responsive factors) [28] and bHLH [72]. Other TFs such as dehydration responsive element binding (DREB) which is a member of the ERF (ethylene-responsive factor) family of transcription factor is not yet fully studied in safflower. Generally, molecular mechanisms of drought tolerance in safflower are still largely unknown.

3.4 Management of Drought

Drought stress management begins with the selection of drought tolerant genotypes and changes in agronomic practices such as planting time, plant population per unit area, and better soil management. Safflower genotypes vary in their response to drought stress and thus genotypes that exhibit excellent drought tolerance characteristics are better suited to be used by farmers because they will save the costs of implementing other drought management strategies. Elucidating genotypes with drought tolerance characteristics aids in the identification of genotypes with desirable traits that could be used for breeding purposes. Plant breeding has contributed to a large extent in tackling the challenges of food security at a global level [73]. In safflower, breeding for drought tolerance has been achieved through conventional breeding which is time consuming. Other breeding methods such as marker assisted breeding and transgenic approach could offer much more benefits in the improvement of drought tolerant safflower genotypes [73]. Other drought stress management approaches are the exogenous application of micro-nutrients (zinc, boron, and iron) which results in enhanced growth, yield, enzymatic and non-enzymatic antioxidant activity [74], [75], osmoprotectants such as ascorbic acid [20] and putrescine [76] and signaling molecules (sodium nitroprusside and salicylic acid) [53]. Supplemental irrigation is an important management practice for increased productivity of safflower especially, under arid and semi-arid conditions [17].

4. CONCLUSIONS AND PERCEPTIVE

Safflower growth and development are greatly reduced under drought stress due to production of smaller organs, inhibited flower and capitula production, and achene filling. Drought stress results in reduced yield and yield components, oil content and yield, and fatty acid composition especially oleic and linolenic acids which determines safflower oil quality. Studies on safflower drought tolerance mechanisms such as biosynthesis of osmoprotectants, enzymatic antioxidants, protective proteins, and transcription factors are still at emerging stages. There are many transcriptional factors and functional proteins that are known to induce drought stress genes in the regulation of plant tolerance to stress, but only a few of them have been studied in safflower. More studies need to be conducted in this area under field conditions where multiple stresses occur at the same time. Such broad knowledge will help to understand the role transcription factors and functional proteins play in the modulation of safflower drought tolerance. Plant drought tolerance techniques are very complex and cannot just be associated with a single metabolic pathway, but a combination of pathways either working independently of each other and/or having a synergistic relationship. The complexity of drought tolerance mechanisms has slowed genetic engineering of drought-tolerant crops. The use of genomics, proteomics, and transcriptomic strategies to better know the molecular control of drought tolerance in safflower plants and efficient water use in water deficit conditions are important. Molecular knowhow of the response and tolerance techniques can pave ways for genetic engineering of safflower plants that can cope and tolerate drought stress leading to sustainable economic yield and fatty acid composition. The use of marker selected breeding and transgenics is suggested to be employed in safflower improvement programs. Exogenous application of plant bioregulators and osmoregulators to plants at different stages of growth and development or seeds may alleviate ramifications of water stress.

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