Drought stress in plants: An overview on implications, tolerance mechanisms and agronomic mitigation strategies

Sadam Hussain*, Saddam Hussain¹, Tauqeer Qadir¹, Abdul Khaliq¹, Umair Ashraf², Abida Parveen³**, Muhammad Saqib⁴ & Muhammad Rafiq⁴

¹Department of Agronomy, University of Agriculture, Faisalabad 38040, Pakistan
²Department of Botany, University of Education, Faisalabad-campus, Pakistan
³Department of Botany, Government College University Faisalabad, Pakistan
⁴Agronomic Research Institute, Ayub Agricultural Research Institute, Faisalabad, Pakistan

Abstract
Drought is considered as one of the major limiting factors affecting growth and productivity of crop plants. It severely affects the morphological and physiological activities of the plants and hampers the seed germination, root proliferation, biomass accumulation and final yield of field crops. Drought stress disrupts the biosynthesis of chlorophyll contents, carotene and decreases photosynthesis in plants. It gradually reduces CO₂ assimilation rates owing to decrease in stomatal conductance. In addition, drought affects cell membrane stability and disrupts water relations of a plant by reducing water use efficiency. To cope with these situations, plants adopt different mechanisms such as drought tolerance, avoidance and escape. In this review, we discussed about the effects of drought on morphological and physiological characteristics of plants and suggested the different agronomic practices to overcome the deleterious effects of drought stress.

Keywords: Antioxidants; Drought; Seed germination; Photosynthesis; Crop yield


Copyright: © Hussain et al (2019). This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited (https://creativecommons.org/licenses/by/4.0/).

Introduction
Different abiotic stresses such as high and low temperature, drought, heavy metals and soil salinity are detrimental to the growth, development and productivity of field crops (1). Drought stress is mainly caused by no or low rainfall in dry or wet season and/or deviation of rainfall pattern from its normal period (2). Alarmingly, 10% of the total land will suffer drought stress during early of 21st century that can be increased up to 40% by the end of this century (3).

Imposition of drought caused morphophysiological, anatomical and molecular changes in plants. Water stress conditions severely affect
the morphology of crops by inhibiting seed germination, and early growth of plants (4, 5). The drought stress reduces the plant biomass accumulation and partitioning, harvest index and productivity of crops (6). Approximately 70% yield in various crops was reduced by drought stress (7, 8).

Different physiological activities in plants such as osmotic adjustment, water relations, photosynthesis and respiration are disturbed under drought stress (9, 10). The mechanism of yield reduction under water stress condition is linked to the reduced light absorption, low photosynthetic rates, water use efficiency (WUE) and harvest index (11).

The level of vulnerability of crop against drought stress depends on its severity, plant genotypes and stage of crop growth (12). Plant survive under limited water supply through several morpho-physiological and biochemical mechanism eg., by changing their architecture, controlling growth rate, adjusting water balance of the cells and tissues and activating the anti-oxidative defense systems (13). This review discusses the effects of drought on morphological and physiological activities of plants and describes the mechanism adopted by the plants to adapt/survive under drought conditions. It also highlights the different agronomic approaches for reducing the effects of drought stress on crop plants under field conditions.

**Effect of drought on plant morphology**

**Seed germination**

Seed requires the proper amount of water for germination, however under water deficit conditions, it is unable to imbibe and germinate even all other external/internal conditions are favorable. Hence, reduced seed germination and poor stand establishment are the primary signs of drought at early crop growth stages (4). Drought stress substantially reduced the germination and stand establishment in various field crops (14, 15).

Many legumes, cereals, and fodder species have shown poor seed germination under drought stress. For instance, poor seed germination and stand establishment were recorded under water deficit conditions in rice and peas (16-18). Moreover, poor germination in Alfalfa (Medicago sativa) was also recorded under drought stress conditions (19). It seems to be clear that water deficit causes poor germination and reduced stand establishment in various field crops. Therefore, adequate moisture supply is an absolute requirement for early growth of various crops.

**Root growth**

A well develop root system helps the plants to anchor as well as uptake of water and nutrients from its immediate vicinity to which it exists. Drought causes apparent modifications in the root architecture and morphological characters in crop plants. Most often, the root growth under mild drought conditions is not severely affected. For example, the root growth in maize was not substantially affected under water deficit conditions (20). However, the root growth under deficit water conditions was increased in Catharanthus roseus (21) and Helianthus annuus (22). On the other hand, a significant decrease in the dry weight of roots in Populus (23) and some species of sugar beet (24) were recorded under severe drought stress. In general, drought stress increased the root-shoot ratio in different plant species (25).

**Leaf area**

Drought stress causes significant reduction in leaf area of many plant species. The increase in leaf area mainly depends on the leaf turgor pressure, canopy temperature and availability of photo-assimilates (26, 27). Leaf area growth is the main factor for photosynthesis and grain yield (28). Water deficit conditions reduced the leaf area by reducing leaf expansion and thus affect the process of photosynthesis (27). Furthermore, the leaf area of maize (29), rice (30), wheat (31), soybean (32) and many other field crops (14) was significantly affected under limited water conditions.

**Leaf rolling**

Leaf rolling is the loss of the potential pressure due to water loss from the upper epidermis of leaf; the phenomenon helps to reduce leaf temperature, interception of incident radiation and transpiration rate (33, 34). Drought stress increased the leaf rolling in different plant species. Drought stress decreased the cell size, stomatal activity, leaf area and increased the leaf rolling (30). A study of two rice cultivars 'IRAT109' (drought tolerant) and 'Zhenshan97B' (drought sensitive) showed that drought stress significantly limited plant height, increased the leaf rolling and reduced the final yield of susceptible cultivar under drought stress (30). Furthermore, studies reported that some agronomic traits for drought response are increased leaf rolling, decreased root-shoot length, relative water contents (RWC), panicle length, grains per panicle and dry biomass accumulation (18).

**Plant height**

The internal plant factors involved to enhance the plant height are substantially affected by drought stress. A decline in plant height could be attributed to the reduction in cell expansion, increase in leaf abscission under drought conditions (5) and impaired mitosis (35). The plant height is largely associated with cell enlargement and leaf senescence. Generally, lower cell enlargement and higher leaf senescence are the basis of reduction in...
plant height. Several studies have been reported that the plant height in different field crops such as wheat (36), maize (29, 37), peas (38), and soybean (39) was decreased under drought stress. Furthermore, drought stress also reduced the height in some fruit plants, for example there are reports on 25% reduction in height of citrus plants grown under water deficit conditions (40). Similarly, plant height of Abelmoschus esculentus decreases with more leaf senescence and less cell enlargement under drought stress (41). A systematic approach should be adopted by conventional breeding instead of traditional breeding to improve plant height of crops being cultivated in drought prone areas.

**Mechanism of growth reduction**

Growth of plant can be accomplished by cell division, cell enlargement and other physiological, ecological as well as morphological events. Plant growth is highly dependent on these events. Drought stress can severely impair these activities. Mechanism of growth reduction under drought stress as; (a) reduced cell turgor pressure, b) abridged water uptake and c) reduced photosynthesis and photo-assimilates required for cell division, mitosis and cell enlargement which often lead to reduction in plant height (14, 35). The phenominal changes in plant growth under drought stress are presented in (Fig. 1). In a study, it has been described that cellular growth is quite sensitive to drought and is severely inhibited by interruption of water flow from xylem to the surrounding cells (142). Abating mitosis, impaired cell elongation and expansion under drought stress are the major factors which reduce the plant height, leaf area and crop growth (15).

![Fig. 1. A schematic representation of plant growth reduction mechanism under water deficit conditions](image)

**Plant biomass and yield**

Drought stress causes significant reduction in dry biomass accumulation and grain yield in different field crops (42). Similarly, imposition of drought stress at silking, grain-filling and maturity stages led to reduce the total dry biomass by 37%, 34% and 21% respectively in maize crop (43). Drought stress generally caused grain yield reduction in all agronomic crops. The yield reduction due to drought stress in different field crops has been listed in (Table 1). The grain yield reduction mainly depends upon the time of the onset of drought and stage of the crop. Similarly, drought stress at flowering and grain filling stages reduced the grain yield in maize (44), green gram and common beans (45), parsley (46) and wheat (47, 48). In addition, drought stress at pre-anthesis stage reduced the grain size and number of grains in wheat (49) whilst after anthesis, it reduced the grain filling period in different cereal crops (50). Furthermore, drought stress at silking stage caused phenological delay between silking and anthesis stages, and reduced the total number of grains and grain yield in maize (43, 51). Drought stress at heading and maturity stages reduced the total dry biomass and grain filling percentage in wheat (52). The enzymes, i.e., starch synthase (SS), adenosine diphosphate glucose pyrophosphorylase (ADGP), starch branching enzyme (SBE) and sucrose synthase (SS) are involved in the grain filling process of cereals (53) and severely affected by drought stress (54, Table 1).

<table>
<thead>
<tr>
<th>Crop</th>
<th>Yield reduction (%)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wheat</td>
<td>64.46</td>
<td>Rizza et al. (55)</td>
</tr>
<tr>
<td>Barley</td>
<td>50</td>
<td>Samarah et al. (56)</td>
</tr>
<tr>
<td>Maize</td>
<td>63-87</td>
<td>Kamara et al. (43)</td>
</tr>
<tr>
<td>Rice</td>
<td>53-92</td>
<td>Lafitte et al. (57)</td>
</tr>
<tr>
<td>Canola</td>
<td>30</td>
<td>Sinaki et al. (58)</td>
</tr>
<tr>
<td>Soybean</td>
<td>46-71</td>
<td>Samarath et al. (59)</td>
</tr>
<tr>
<td>Pigeon pea</td>
<td>40-55</td>
<td>Nam et al. (60)</td>
</tr>
<tr>
<td>Cowpea</td>
<td>55-65</td>
<td>Ogbonnaya et al. (61)</td>
</tr>
<tr>
<td>Chickpea</td>
<td>45-69</td>
<td>Nayyar et al. (45)</td>
</tr>
<tr>
<td>Sunflower</td>
<td>60</td>
<td>Mazahery-Laghab et al. (62)</td>
</tr>
</tbody>
</table>

**Effect of drought on plant physiology**

**Chlorophyll contents**

Chlorophyll is the main component of chloroplast which plays a significant role in the photosynthesis. Chlorophyll pigments are essential for the plants to capture light and utilize in the functioning of photosynthesis (9). Under water deficit conditions, the chlorophyll contents have considerably reduced due to enhanced oxidative stress and/or deterioration or photo-oxidation of the chlorophyll pigments. Drought stress considerably reduced the functioning of both chlorophyll a and b (14, 37). In a study it has also been identified that the reduction of chlorophyll a, b and total chlorophyll contents of sunflower under drought conditions (63). Likewise, the chlorophyll contents were sharply reduced i.e., 29% and 42% in Chemlali and Chétoui olive cultivars, respectively under drought stress (64). The chlorophyll contents were reduced in response to the water deficit conditions in mesophyll cells of the leaf and a small amount are
also decreased through bundle sheath cells (65). In fact, the drought conditions severely affect the biosynthesis and functioning of the chlorophylls in plants that could have severe consequences on photosynthetic machinery and assimilate partitioning. Different metabolic processes and activities are disturbed by drought stress which in turn lead to reduction in chlorophyll contents. This reduction can also be attributed to the inhibition of biosynthesis of precursors of chlorophyll under drought stress (143). Drought stress may also cause severe reduction of sodium and potassium contents of root and shoot (143). Owing to stomatal closure under drought stress, absorption of CO₂ is limited which may promote the imbalance between the electron requirement of Calvin-Benson cycle and photochemical activity of photosystem II and result into photo-inhibitory damage to reaction centers of PSII (144).

**Carotenoids**

Several studies have reported a decrease in carotenoids contents in various crops under drought stress (63, 145-148). Carotenoids are grouped into hydro-carbon carotenes, consisted on lycopene and xanthophylls or β-carotene and they are characterized by lutein (66). They play a major role in anti-oxidant protection system but highly susceptible to the over-activation of reactive oxygen species (ROS) (28). The enzymatic antioxidant system together with non-enzymatic system i.e., β-carotenes, α-tocopherol, ascorbate, reduced glutathione and enzymes containing ascorbate peroxidase, peroxidase, polyphenol oxidase, catalase and glutathione reductase provide protection to carotenoids against ROS (67). β-carotene directly involved in the reduction of triple chlorophyll which inhibits the generation of the singlet oxygen and thus protects from oxidative damage (14). Additionally, β-carotene plays a main role in protecting and sustaining photochemical processes as well (68).

**Photosynthesis**

Drought stress hampered the photosynthetic system by altering CO₂ conductance through stomata, carbon cycle, electron transport chain (ETC) of thylakoid membrane, membrane lipid peroxidation and water imbalance (1, 69). Under water deficit conditions, limited gaseous exchange causes a reduction in leaf growth, premature leaf abscission, oxidation of protein and limited photosynthesis (70). According to a study, drought in maize led to significant reductions in net photosynthesis, transpiration, stomatal conductance, inter-cellular CO₂, water use efficiency, and intrinsic water use efficiency as compared with the well-watered crop (37). The mechanism of photosynthesis reduction in plants under drought stress is as: i) reduction in chlorophyll biosynthesis, ii) stomatal closure through ABA signaling which reduce carboxylation process, iii) reactions of ROS with the cellular lipids and proteins, and iv) reduced RuBP and PEP-case activity (14). Hence, drought caused reduction in photosynthesis is an intricate phenomenon that is affected by various intrinsic and extrinsic factors.

**Respiration**

Drought often causes reduction in the rate of respiration in different plant parts such as leaves (71), shoots (72), roots (73), flower apices (74) and in whole plant as well (75-77). Several researchers described the unaffected (78), or increase (79, 80) rate of respiration in plants under the limited water supply. However, all kinds of respiration were stopped at low water potential (~35 bars) (10). The soil selection under limited water supply is important for respiration of many plant species. Similarly, according to Collier and Cummins (81) rate of respiration in leaves is also slow when plants are grown on high organic soils, as compared to the vermiculite soil, in which drought conditions develop very rapidly.

**Stomatal conductance**

Responses of stomatal conductance are more likely to be associated with the soil moisture than leaf moisture contents. However, gaseous exchange through stomata is not only affected by the soil water content but also other external and internal plant factors (14). Severity in drought stress causes intensively caused stomatal closure and thus reduces net photosynthesis. A study conducted on Chinese Hibiscus revealed that under limited soil water contents, the rate of transpiration, stomatal conductance, water-use efficiency and RWC were decreased (82).

**Cell Membrane Stability (CMS)**

The cell membrane stability (CMS) can be used as an index of selecting drought tolerant genotypes (17). CMS and cell membrane integrity under water deficit conditions propose resistance against water stress. Genotypes having lower the CMS values showed higher vulnerability to drought stress and vice versa (83). Similarly, CMS index is substantially important in breeding programmes and predicts drought tolerance or sensitivity criteria (84). The genotypes with <50% value for CMS are more vulnerable to drought, whereas genotypes having CMS values ranged 71-80% showed more potential towards drought tolerance (83). Under limited water supply, CMS showed positive association with tillering ability and grain yield of wheat, but negative with 1000-grain weight (85). Furthermore, drought activates the oxidative process in plant species which finally reduces the membrane stability owing to lipid peroxidation (70), and consequently damages the cell membrane (86).

**Water use efficiency**

The proportion between dry-matter produced and the amount of water consumed is known as water
use efficiency (WUE) of that plant (87). Plant water status is the measure of relative water content (RWC) and the RWC mostly depends on the water uplifting by the plant roots and transpiration rate by the plant leaves and temperature. Furthermore, water deficit conditions considerably reduce the water potential of leaf, transpiration rate and RWC with increasing temperature in plants (88). Moreover, leaves respond quickly to drought and by lowering the water potential and RWC rapidly. Similarly, the leaves of plants which are exposed to the water deficit condition, shown more decline in the RWC and water potential (89). Under limited water condition, the total water content of Barbary fig decreased by 57% (90). Wheat WUE was higher under drought stress than well-watered conditions (91, Table 2).

Table 2. Effect of soil water contents on relative water contents, transpiration, and photosynthesis in different plants

<table>
<thead>
<tr>
<th>Crop</th>
<th>Soil water content</th>
<th>RWC (%)</th>
<th>Transpiration (mmol m⁻² s⁻¹)</th>
<th>Photosynthesis (mol m⁻² s⁻¹)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter wheat</td>
<td>Well-watered</td>
<td>79.4 ± 1.93</td>
<td>6.0 ± 0.58</td>
<td>9.7 ± 0.02</td>
<td>Roohi et al. (92)</td>
</tr>
<tr>
<td></td>
<td>Water deficit</td>
<td>70.1 ± 3.25</td>
<td>3.51 ± 0.44</td>
<td>5.1 ± 1.19</td>
<td></td>
</tr>
<tr>
<td>Soybean</td>
<td>100%</td>
<td>-</td>
<td>11.6</td>
<td>17.45</td>
<td>Purwanto (93)</td>
</tr>
<tr>
<td></td>
<td>50%</td>
<td>-</td>
<td>5.5</td>
<td>8.67</td>
<td></td>
</tr>
<tr>
<td></td>
<td>25%</td>
<td>-</td>
<td>0.7</td>
<td>1.81</td>
<td></td>
</tr>
<tr>
<td>Winter barley</td>
<td>Well-watered</td>
<td>77.4 ± 5.03</td>
<td>4.9 ± 0.91</td>
<td>7.9 ± 2.47</td>
<td>Roohi et al. (92)</td>
</tr>
<tr>
<td></td>
<td>Water deficit</td>
<td>59.8 ± 5.09</td>
<td>2.8 ± 0.41</td>
<td>3.6 ± 0.92</td>
<td></td>
</tr>
<tr>
<td>Soybean</td>
<td>Well-watered</td>
<td>83.5 ± 5.02</td>
<td>53 ± 0.26</td>
<td>8.8±0.64</td>
<td>Roohi et al. (92)</td>
</tr>
<tr>
<td></td>
<td>Water deficit</td>
<td>71.3 ± 1.37</td>
<td>3.19 ± 0.38</td>
<td>5.3 ±0.70</td>
<td></td>
</tr>
</tbody>
</table>

RWC: relative water contents

Drought mitigation mechanisms

Morphological approaches

The most common morphological approaches of plants for drought resistance are; drought tolerance, drought avoidance and drought escape (Fig. 2) (94, 95). The drought tolerant plants continue to function normally by maintaining turgor even at low water potential (96). Osmoregulation, osmoprotectants synthesis, osmolyte accumulation and antioxidant activities are the responses of plants against drought stress (96, 97). The capability of a plant to complete its life cycle earlier than drought period is termed as drought escape (98). This involves early germination, faster plant growth, flowering and maturity.

The drought avoidance mechanism allows plants to evade dehydration by maintaining internal water status of plants (94, 99, 100). Decrease in leaf number and size, leaf rolling, and leaf orientation can reduce the water losses and radiation absorption in plants (101-103). Moreover, by improving leaf waxiness, deep and high rooting density often increases water uptake deep from the soils (104-106).

Biochemical mechanisms

Proline activity

Turgor pressure of the cell is maintained by the concentration of different solutes, which lesser the osmotic potential of cytosol (107). Proline often determines the association and conservation of the protein structure, hold the membrane’s structure under water deficit condition and inhibit the photo-inhibition (108). It also helps to maintain the sub-cellular structures, cleansing of free radicals, mitigating the oxidation-reduction potential (109)
and regulate mitochondrial purposes through the act as signaling molecular substance under drought stress. Additionally, it also determines the cell development and cell death and activates the particular gene aspects which are necessary for retrieval of the plant from drought stress (110).

The mechanism of proline under drought is depicted in (Fig. 3). Under limited water condition, the maintenance of cell turgor pressure can be attained by the regulation of osmotic potential by synthesizing proline, carbohydrate, sucrose, glycine-betaine, and other solute-substances in the cytoplasm. Increased proline contents were directly associated with drought tolerance in wheat (111). Similarly, in maize, the proline percentage increases as the water deficit condition prolonged and reached to its peak 10 days after imposition of drought, but reduced under the acute water stress (37).

**Molecular mechanisms**

Low availability of water in soil may lead to cellular water deficit in plants. Up- and down-regulation of gene expression can take place under these conditions. In response to water deficit conditions, the activity of a number of genes is triggered which enhances the plants’ tolerance to drought stress (149). Gene expression may also be triggered as a result of injury and/or triggered directly as a result of other biotic and abiotic stresses. It is also well documented that plants’ ability to tolerate drought is a multiplex phenomenon and is an outcome of expression of multiple genes.

**Aquaporins**

Aquaporins (AQs) have the ability to facilitate the protein mediated membrane transport in plants (14). Although, different studies demonstrated the understanding of AQs and plant water relation in plants (150), however relation between AQs and crop resistance to drought stress has not been fully illustrated. Maurel and Chrispeels (150) reported that under water deficit conditions, AQs can increase the water permeability by regulating the hydraulic conductivity of membranes.

In a recent year, different researchers carried studies on plant water relations and AQs in plants. Different reports clearly indicate that AQs play important role in uptake of water through plants roots by declining root hydraulic conductivity (151), and play a major role in cellular osmoregulation (152). More expression of plasma membrane AQs in tobacco was reported which improved the plant vigor of tobacco however, overexpression of prolactin-inducible protein 1b gene caused fast wilting under drought stress (152, 153). Different reports demonstrated the specific functions and regulation of intrinsic AQs of plasma membrane. For instance, their overexpression in roots have been reported which can mediate the soil water uptake by roots, and down-regulation of prolactin-inducible protein in trans genetic plants have lower water uptake capacity of plants (151, 152).

**Stress proteins**

To cope with drought stress, the synthesis of different proteins has been reported. Among these proteins, mostly are water soluble and thus enhance the stress tolerance by hydration of cellular structure (154). A variety of stress proteins are implicated under drought which enhance the tolerance capability of plants (53). The induction of dehydration-responsive element-binding genes (DHG) (dehydration-responsive element-binding gene1 and dehydration-responsive element-binding gene2) under dehydration (155). These genes are involved in signal pathways under stressed conditions. The manipulation of these genes in plants may enhance the drought tolerance ability of these plants (156). Previous studies have reported drought tolerance in rice and groundnut by manipulation of DHG (157, 158). Apart from
DHG, different capsella bursa-pastoris like genes are also synthesized under drought stress (159). Introduction of DHG in transgenic tall fescue may result in more accumulation of proline which increases the drought resistance in crops. This phenomenon indicates the ability of capsella bursa-pastoris 3 to induce tolerance against drought (160). The expression of some dehydrins and late embryogenesis abundant genes have also been reported under drought stress (161). Low-molecular-weight heat shock proteins also play a role in increasing the capability of plants to cope with abiotic stresses (154, 162). Different membrane-stabilizing proteins are another group of protein which is responsible for enhancing the drought tolerance in various crops. These increase the water-binding capacity by creating a protective environment and also play an important role in the sequestration of ions (163).

Different Agronomic Practices to overcome the drought effects

Changing the sowing time

Planting date is an important factor regarding drought escape in subtropical, tropical and rained conditions (112). Early planting under dry conditions is corrected by improving WUE, changing the sowing time so that plant does not suffer drought stress specially at critical stages (100). The cropping system that provides balance and adequate water with an appropriate quantity of nutrients will improve canopy growth and yield by enhancement of biomass production. The more of canopy area, the more will be the evapotranspiration (113). Consequently, changes in the production of biomass through each unit of transpiration by adjusting planting dates can be a helpful strategy for drought tolerance or drought escape (114).

Adequate supply of Irrigation and Soil amendments

Topsoil modifications affect soil water by infiltration, evaporation and environment-soil heat transfer (115). Water can be preserved in soil by different means and mulching is one of them which can substantially reduce the evaporative losses while could enhance the uptake and storage of water in plant root zone (115, 116).

The current irrigation systems, likewise, drip, film hole and sprinkler irrigation are more efficient and water saving techniques that improve WUE and grain yield as compared to the surface irrigation (115, 117). Therefore, modern irrigation techniques are more suitable for supplying adequate irrigation needed for plant growth and development. The modern irrigation systems are more suitable for cash crops, through delivering the proper amount of water for plant growth under sloppy areas (118). Furthermore, crop yield can be enhanced up to 70% by providing supplemental irrigation and soil management practice at the reproductive growth stage (115).

Seed priming

Seed priming is the most pragmatic and short-term strategy to reduce the effects of drought stress in crop plants (14, 147, 164, 165; Table 3). A partial hydration of seed towards a point associated with a start of metabolic processes of germination but no radicle emergence occur is known as seed priming (119). Better and uniform germination was found in primed seeds (15). Osmopriming with saturated CaHPO$_4$ and KCl (4%) solution resulted in improved germination, better stand establishment and yield of direct seeded rice under water stress conditions (120). Similarly, primed seed of rice showed better germination, rapid seedling establishment and uniform crop architecture that led to the improved yield (4). Under water deficit conditions, primed wheat seeds showed 44% more germination than unprimed seeds (121).

Table 3. Various seed priming techniques adopted for developing drought tolerance in plants

<table>
<thead>
<tr>
<th>Plants</th>
<th>Priming method</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wheat</td>
<td>Hydropriming, auxin priming, halopriming (CaSO$_4$), chemical priming (KH$_2$PO$_4$, H$_2$O$_2$, SNP), gibberellic acid (GA$_3$) priming</td>
<td>Das and Choudhury (122); Ghana and Schillinger (123); Akbari et al. (124); Wahid et al. (125)</td>
</tr>
<tr>
<td>Rice</td>
<td>Hydropriming, PEG, KCl, CaCl$_2$, ascorbate, priming</td>
<td>Basra et al. (126); Farooq et al. (127); Yari and Sheidaie (128); Yuan-Yuan et al. (129)</td>
</tr>
<tr>
<td>Maize</td>
<td>Chemical priming (CuSO$_4$, ZnSO$_4$), on-farm seed priming</td>
<td>Murungu et al. (130); Finch-Savage et al. (131); Foti et al. (132); Janmohammadi et al. (133)</td>
</tr>
<tr>
<td>Sugarcane</td>
<td>Halopriming (NaCl)</td>
<td>Patade et al. (134)</td>
</tr>
<tr>
<td>Cotton</td>
<td>Hydropriming, hormonal (GA$_3$)</td>
<td>Murungu et al. (130); Casenave and Toselli (135); Akbari et al. (124)</td>
</tr>
<tr>
<td>Chickpea</td>
<td>Hydropriming, osmopriming (mannitol)</td>
<td>Kaur et al. (136, 137); Elloca et al. (138)</td>
</tr>
<tr>
<td>Sunflower</td>
<td>Hydropriming, osmopriming (KNO$_3$)</td>
<td>Kaya et al. (15)</td>
</tr>
<tr>
<td>Mustard</td>
<td>Hydropriming, NaCl, priming, ABA priming</td>
<td>Srivastava et al. (139, 140)</td>
</tr>
<tr>
<td>Canola</td>
<td>Hydropriming</td>
<td>Omidi et al. (141)</td>
</tr>
</tbody>
</table>

Conclusions

Drought stress often resulted in substantial loss in growth and yield agronomic crops. Drought stress impedes various morphological and physiological processes in different crops. It generally reduces seed germination and impairs stand establishment, reduces leaf area, overall plant growth and total dry biomass accumulation in different crops. Drought stress hampers the
photosynthetic and gas exchange attributes chlorophyll biosynthesis and cell membrane integrity as well as alterations in phenological development of crops. Plants respond to water deficit conditions by drought avoidance and tolerance mechanism eg., by changing their leaf shape, leaf number and size, leaf rolling and leaf orientation which helps to reduce water losses and light interception in plants. Osmoregulation, osmo-protectants biosynthesis, accumulation of compatible solutes and antioxidant activities are the bio-physio-chemical responses of plants to drought stress. Different agronomic practices such as changing the sowing times, efficient use of irrigation water and seed priming techniques can be quite helpful to minimize the effect of drought stress under field conditions.

Authors’ contributions
All authors contributed to the content of the manuscript and approved the final version.

Competing Interests
The authors declare that they have no competing interests.

References


https://doi.org/10.2135/cropsci1980.0011183X0002000020001x


https://doi.org/10.2135/cropsci1972.0011183X00012000040002x

https://doi.org/10.1111/j.1399-3054.1996.tb00216.x

https://doi.org/10.1007/s11099-005-5404-2


https://doi.org/10.1046/j.1439-037x.2004.00592.x


https://doi.org/10.1046/j.1439-037x.2000.00035.x

https://doi.org/10.1007/s11356-018-1855-x

https://ejournal.sinica.edu.tw/bbacs/content/2000/1/bot1 46.html

https://doi.org/10.1016/j.envexpbot.2005.06.021


https://doi.org/10.2135/cropsci2004.4740


https://doi.org/10.1111/j.1438-8677.2007.01727.x

https://doi.org/10.1007/s13593-015-0283-4


https://doi.org/10.1080/000521130171015-2


Kiran S, Yin H, Peng S, Khan FA, Khan F, Huang J, Cui K, Nie L. Comparative transcriptional profiling of...

