

REVIEW ARTICLE

Drought Stress in Grain Legumes during Reproduction and Grain Filling

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Keywords

marker-assisted selection; osmotic adjustment; photosynthesis; terminal drought

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Accepted December 18, 2015

doi:10.1111/jac.12169

Abstract

Water scarcity is a major constraint limiting grain legume production particularly in the arid and semi-arid tropics. Different climate models have predicted changes in rainfall distribution and frequent drought spells for the future. Although drought impedes the productivity of grain legumes at all growth stages, its occurrence during reproductive and grain development stages (terminal drought) is more critical and usually results in significant loss in grain yield. However, the extent of yield loss depends on the duration and intensity of the stress. A reduction in the rate of net photosynthesis, and poor grain set and grain development are the principal reasons for terminal drought-induced loss in grain yield. Insight into the impact and resistance mechanism of terminal drought is required for effective crop improvement programmes aiming to improve resistance to terminal drought in grain legumes. In this article, the impact of terminal drought on leaf development and senescence, light harvesting and carbon fixation, and grain development and grain composition is discussed. The mechanisms of resistance, management options, and innovative breeding and functional genomics strategies to improve resistance to terminal drought in grain legumes are also discussed.

Introduction

Grain legumes are an important and cheap source of protein, which play a distinct role in agricultural ecosystems with their ability to fix nitrogen (N) symbiotically (Siddique et al. 1999, Rubiales and Mikić 2015). This special trait makes them excellent colonizers of low N environments (Graham and Vance 2003). Grain legumes also have, among others, industrial and medicinal uses. The most important grain legumes are chickpea (*Cicer arietinum* L.), mashbean (*Vigna mungo* L.), common bean (*Phaseolus vulgaris* L.), mungbean (*Vigna radiata* L.) and soyabean (*Glycine max* L.). Grain legume production is threatened by various environmental stresses (Vyas 2014), of which water deficit has been identified as an important factor limiting crop productivity worldwide (Turner et al. 2005, Micheletto et al. 2007, Fang et al. 2010).

Grain legumes are more prone to drought as they are mostly grown in rainfed production systems, and global climate models have predicted increases in the intensity and frequency of drought episodes (Rosenzweig and Colls 2005). While drought at any point in the crop cycle can affect crop growth thus reducing grain yield, any water deficit during reproduction and grain filling (terminal drought) is more devastating (Delmer 2005, Pushpavalli et al. 2014). Terminal drought occurs when soil moisture recedes – mostly during pod filling, but can start well before flowering (Subbarao et al. 1995, Delmer 2005, Fang et al. 2010, Pushpavalli et al. 2014). In eastern India, terminal drought frequently affects productivity of grain legumes. Intermittent drought occurs as a result of finite periods of inadequate irrigation or breaks in winter rainfall (Samarah et al. 2009).

Moderate to severe drought reduces plant biomass, grain yield and related components of legumes (Siddique et al.

2001, Ghassemi-Golezani and Mardfar 2008, Demirtas et al. 2010, Baroowa and Gogoi 2013, Ghassemi-Golezani et al. 2013, Table 1). The magnitude of the reduction depends on the duration and intensity of the stress, genotypic variability and crop developmental stage. For instance, there were significant differences in grain yield of chickpea when irrigated at flower initiation and pod filling stages and inferred that later is more sensitive to water deficit, but any water deficiency may cause considerable yield loss (Shamsi et al. 2010). Therefore, developing strategies to enhance terminal drought resistance in grain legumes is pivotal for reducing yield losses in drought-affected areas. Development of genotypes with better water-use efficiency (WUE) may help to improve grain yield in dry environments (Ulemale et al. 2013).

The generation and diffusion of appropriate technologies for diverse production environments is the cause of increase in grain legume production in developed part of the world. Technologies such as developing traits for drought resistance, breeding for shorter duration and water efficient approaches such as use of polythene mulching and drip irrigation are among those (Beebe et al. 2013).

There are several reviews on the effects of drought stress on different physiological and biochemical aspects of grain legumes (Subbarao et al. 1995, Vyas 2014). However, no comprehensive and updated review is available describing the effects and resistance mechanisms of drought in grain legumes. This review discusses the impact of terminal drought on grain legumes including the effects on leaf development, carbon fixation and grain yield, and physiological resistance mechanisms. Management options, as well as innovative breeding and functional genomics

strategies to improve resistance to terminal drought in grain legumes are also included.

Effects of Terminal Drought

Grain legumes vary in their sensitivity to terminal drought, but in all cases grain yield is substantially reduced (Table 1). This drought-induced reduction in grain yield is associated with leaf senescence (Lopez et al. 1997), oxidative damage to photosynthetic apparatus (Farooq et al. 2009), reduced carbon fixation and assimilate translocation (Mondal et al. 2011, Zlatev and Lidon 2012), inhibited flowering and reproductive development (Samarah et al. 2009), sterility of pollen grains (Al-Ghzawi et al. 2009), reduced grain set and development (Croser et al. 2003, Liu et al. 2004, Vadez et al. 2012) and reduced sink capacity (Andersen et al. 2002).

Leaf senescence

Drought stress impacts many aspects of plant growth including leaf initiation and expansion, as these processes are severely disturbed due to soil water deficit. Water stress reduces the production of new leaves and promotes senescence and abscission (Karamanos 1980). As a consequence, total leaf area drastically decreases. Under drought, gradual senescence of older leaves is often observed before younger leaves. Drought-induced leaf senescence occurs gradually and is the outcome of a highly coordinated programmed process. In drought-stressed plants, leaf senescence is characterized by leaf chlorosis, and changes in ultrastructure and metabolism. The whole process is controlled by the

Table 1 Reduction in economic yield by drought stress in some important grain legumes

Crop	Growth stage	Yield reduction (%)	References
Mashbean (<i>Vigna mungo</i> L.)	Flowering	31–57	Baroowa and Gogoi (2014)
	Reproductive	26	Baroowa and Gogoi (2013)
Chickpea (<i>Cicer arietinum</i> L.)	Late ripening	49–54	Samarah et al. (2009)
	Anthesis	27–40	Mafakheri et al. (2010)
	Reproductive	45–69	Nayyar et al. (2006)
Common bean (<i>Phaseolus vulgaris</i> L.)	Reproductive	58–87	Martínez et al. (2007)
	Flowering	49	Rosales-Serna et al. (2004)
	Pod filling	40	Ghanbari et al. (2013b)
Cowpea (<i>Vigna unguiculata</i> (L.) Walp.)	Reproductive	34–66	Ahmed and Suliman (2010)
	Pod filling	29	Akyaempong (1986)
Faba bean (<i>Vicia faba</i> L.)	Grain filling	68	Ghassemi-Golezani and Hosseinzadeh-Mahootchy (2009)
Lentil (<i>Lens culinaris</i> L.)	Reproductive	24	Allahmoradi et al. (2013)
	Pod development	70	Shrestha et al. (2006)
Pigeon pea (<i>Cajanus cajan</i> L.)	Flowering	42–57	Nam et al. (2001)
Soyabean (<i>Glycine max</i> (L.) Merr.)	Grain filling	42	Maleki et al. (2013)
	Onset of pod set (R ₃)	45–50	Kobraee et al. (2011)

endogenous levels of plant hormones including abscisic acid (ABA), cytokinins, jasmonates, salicylates and ethylene (Munné-Bosch and Alegre 2004).

For many grain legume species, leaf area development is more sensitive to soil moisture deficit than leaf abscission (Muchow 1985). However, a strong correlation exists between drought-induced reduction in leaf area development and the degree of leaf senescence (Lopez et al. 1997). In cowpea and pigeon pea, drought stress during flowering and pod filling caused senescence and abscission of mature basal leaves (Lopez et al. 1997). Severe drought accelerates leaf senescence due to reduced nitrogen (N) uptake, and therefore reduced chlorophyll biosynthesis and radiation use efficiency (De Souza et al. 1997). As the patterns of acropetal leaf senescence from drought and monocarpy are similar in cowpea, their combined effect appears to accelerate senescence under drought (Gwathmey and Hall 1992).

Light harvesting and carbon fixation

Drought impacts the photosynthetic apparatus, by essentially disrupting all of its major components including stomatal control of CO₂ supply, electron transport and carbon reduction cycle (Allen and Ort 2001, Awasthi et al. 2014). Water deficit reduced nutrient (particularly N) uptake causing alkalization of xylem sap, leading to increased apoplastic ABA concentration with concomitant stomatal closure (Liu et al. 2005). This entire process of interference with photosynthesis may occur through stomatal or non-stomatal mechanisms (Farooq et al. 2009).

Stomatal control of water loss is an early plant response to drought resulting in deprivation of carbon influx by leaves (Chaves 1991, Awasthi et al. 2014). The lower internal CO₂ concentration during drought is responsible for reductions in photosynthesis by inhibiting the enzyme at the acceptor site of ribulose-1, 5-bisphosphate carboxylase/oxygenase (Rubisco) or by direct inhibition of photosynthetic enzymes such as Rubisco or ATP synthase (Zlatev and Lidon 2012). The strong correlation of mesophyll photosynthesis with stomatal aperture also indicates down regulation of photosynthetic apparatus due to low carbon supply. The good correlation between leaf water potential and stomatal conductance even under drought supports this assumption (Farooq et al. 2009).

Partial stomatal closure or collapse of mesophyll cells due to turgor loss shows heterogeneity in leaf photosynthesis during drought (Farooq et al. 2009). This situation suppresses the carboxylation reaction and regeneration of ribulose-1, 6-bisphosphate (RuBP) with concomitant increase in photorespiration. The over-reduction in components within the electron transport, following a substantial loss in intercellular CO₂ during water deficit, results in transfer of electrons to oxygen at photosystem I (PSI),

which generates reactive oxygen species (ROS). Such ROS include superoxide, hydrogen peroxide and the hydroxyl radical, which may lead to photo-oxidation if the plant is not efficient in scavenging these molecules. Several *in vivo* studies have demonstrated damage to the oxygen-evolving complex of photosystem II (PSII) under drought. The non-stomatal response of carbon fixation such as PSII energy conversion and the dark reaction of Rubisco carbon fixation are resistant to drought (Chaves 1991).

Grain development

The effect of water scarcity on yield is a highly complex phenomenon and involves processes as diverse as reproductive organs – gametogenesis, fertilization, embryogenesis – and grain development (Farooq et al. 2009, 2014). Of the plant developmental stages, flowering and reproductive development are especially sensitive to drought (Samarah et al. 2009, Fang et al. 2010). However, the magnitude of flower abortion varies with flower position on the plant (Fang et al. 2010). For instance, within individual racemes in soyabean (*Glycine max* (L.) Merr.), proximal positions exhibit higher pod set than distal positions (Kokubun and Honda 2000) due to reduced assimilate supply at the distal part of the raceme (Mondal et al. 2011).

Drought also reduces flower development time, causing small flowers with nectar of low quality and quantity. Although this situation invites only a few pollinators (Al-Ghzawi et al. 2009), it does not hinder pollination as grain legumes self-pollinate; nonetheless, it prevents embryo development due to lack of photosynthates. Drought also causes pollen grain sterility (Al-Ghzawi et al. 2009) and reduces pollen grain germination and pollen tube growth (Fang et al. 2010, Gusmao et al. 2012). Drought-induced carbohydrate deprivation, enhanced endogenous ABA concentration, and the impaired ability to use sucrose and starch by reproductive sinks are potential factors contributing to pollen grain sterility, abnormal pollen grain and ovary abortion in grain legumes. Accumulation of non-reducing sugars and failure to build up starch during drought leads to ovary abortion, and reduced grain set and grain yield (Andersen et al. 2002). Acid invertase is a key enzyme in grain development; its activity is often lowered with reductions in tissue water potential. Hence this enzyme is considered a limiting factor in starch biosynthesis and ovary development (Farooq et al. 2015). Inadequate energy sources and increased ABA levels during drought are responsible for poor seed set (Liu et al. 2004).

Most grain legumes are indeterminate, which allows for sufficient reproductive sinks to yield satisfactorily (Turner et al. 2005, Vadez et al. 2012). Mild water deficit can shorten this prolonged reproductive growth to facilitate accumulation of more photoassimilates in reproductive

structures and hence higher yields (French and Turner 1991). However, terminal drought strongly affects the capacity to produce a large number of flowers and to set seeds; thus, grain yield is substantially reduced (Pushpavalli *et al.* 2014). For instance, under terminal drought, grain yield in chickpea decreased from 42 % to 70 % (Leport *et al.* 1998, Shrestha *et al.* 2006) owing to pod abortion (Leport *et al.* 1998, 2006, Behboudian *et al.* 2001), reduced pod production (Behboudian *et al.* 2001) and reduced the grain-filling duration (Davies *et al.* 1999). A reduction in water potential and increase in ABA content in flowers and developing pods causes pod abortion (Liu *et al.* 2003, 2004). In common bean, the presence of lower-placed older fruit regulated an increase in ABA content of higher-placed younger fruit, which induced their abortion (Liu *et al.* 2004). The experimental removal of older fruits reduced ABA content in younger fruit and reduced their abortion (Tamas *et al.* 1979). Drought-induced reduction in the time for grain filling resulted in smaller grains in chickpea (Davies *et al.* 1999).

Under drought, rhizobia undergo morphological changes, leading to a reduction in infection and nodulation of legumes (Busse and Bottomley 1989). In faba bean, reduced soil moisture substantially reduced the number of infection threads. Drought also decreased external diameter and caused loss of lenticels in soyabean nodules (Davis and Imsande 1988). Guerin *et al.* (1990) indicated that exposure of faba bean plants to drought resulted in loss of turgor in the nodule cortex – leading to deformation of outer cortical cell. Drought also affects symbiotic nitrogen fixation by increasing oxygen diffusion resistance to root bacteroides leading to less nitrogenase activity. This results in less nitrogen for protein biosynthesis – a key product for grain legumes – and reduces grain yield (Purcell and King 1996).

Grain composition

Legume grains provide an exceptionally varied nutrient profile for humans and livestock, including proteins, amino acids, fibres, vitamins and minerals (Mitchell *et al.* 2009). The carbon energy supply required for germination is stored in seeds mainly in the form of lipids in soyabean or starch in common bean, pea, faba bean, lentil, chickpea, cowpea and mungbean. Drought not only affects grain development but also grain composition. Drought-induced inhibition of protein biosynthesis is responsible for the loss in quality of grain legume seeds. Inhibition of both partitioning and fixation of N in water-limited environments reduces protein accumulation in legume grains (Singh 2007).

Earlier research reported that seed protein content depends highly on genetic background and environmental factors, particularly drought and heat stress, during grain

filling (Rharrabti *et al.* 2001, Tea *et al.* 2004). In an experiment conducted by Ghanbari *et al.* (2013a), drought reduced Fe, Zn, P and N contents and hence total protein in seeds of common bean. A considerable reduction in seed N and protein content was noted in white, red and chitti bean cultivars subjected to drought during pod filling (Ghanbari *et al.* 2013b).

Drought altered fatty acid composition in soyabean, which affected total oil levels, stability of oil and oil composition especially during seed filling (R5–R6) (Bellaloui *et al.* 2013). In addition, the concentration of non-structural carbohydrates such as glucose, fructose and sucrose decreased under drought; the authors concluded that the alteration to fatty acids was due to limited availability of sugars in the plants and translocation from leaves to seeds during seed filling. In another experiment, severe drought stress during grain filling in soyabean reduced oil content by up to 12.4 % with a simultaneous decrease in oleic acid content (Dornbos and Mullen 1992). Deficiency in soil moisture during flowering and pod filling increased the free amino acid pool and inhibited incorporation of amino acids into the protein chain thereby lowering the protein–amino acid fraction in cowpea seeds (Labanauskas *et al.* 1981).

Physiological Basis of Resistance to Terminal Drought

Drought resistance has two broad categories: (i) dehydration avoidance involving morphological adaptations and physiological mechanisms that enable maintenance of tissue water status, and (ii) dehydration tolerance involving remobilization of stem reserves and accumulation of certain protectants that allow proper, or at least partial, functioning under water deficit conditions (Levitt 1972) (Table 2). A brief overview of terminal drought resistance mechanisms in grain legumes is discussed below.

Drought escape and avoidance

Drought escape is a primary crop adaptation strategy to water deficit. Legumes can escape drought by shortening their growth period to avoid the stress by maintaining high tissue water potential by reducing water loss from plants and/or improving water uptake (Siddique *et al.* 1993).

Drought escape occurs when phenological development is successfully matched with periods of soil moisture availability, where the growing season is shorter and terminal drought stress predominates (Farooq *et al.* 2009, 2014). Early flowering and seed set before the onset of terminal drought is an important trait in grain legumes in this regard (Thomson *et al.* 1997). Legumes with an indeterminate growth habit (like cowpea and common bean) may attenuate the effect of temporary drought by producing

Table 2 Potential traits/characters for screening grain legumes for drought resistance

Crop species	Trait	Correlation with yield	References
Chickpea	Prolific root system	Yes	Kashiwagi et al. (2006)
	Shorter growth duration	–	Saxena et al. (1993)
	Smaller leaf area	–	Serraj et al. (2003)
Common bean	Grain size, early maturity and short stature	Yes	Singh et al. (1995)
	Leaf RWC	Yes	Kumar et al. (2006)
	Rooting depth	–	White and Castillo (1988)
	Canopy biomass, pod partitioning index, stem biomass reduction and pod harvest index	Yes	Rao et al. (2013)
Cowpea	Short duration and erect plant type	Yes	Hall (2012)
Faba bean	Earliness and vigorous growth	–	Khan et al. (2010)
Mashbean	Dry matter partitioning	–	Bushby and Lawn (1992)
Lentil	Dry root weight and root length	Yes	Kumar et al. (2012)
Pea	Root osmotic adjustment	–	Greacen and Oh (1972)
Pigeon pea	Extra short duration	Yes	Nam et al. (1993)
	Leaf area maintenance	Yes	Lopez et al. (1997)
	Root and shoot biomass	Yes	Chauhan et al. (1998)
	Osmotic adjustment	Yes	Lopez et al. (1987)
Soyabean	Presence of dense leaf pubescence	–	Balochi et al. (1985)
	Carbohydrate store and remobilization	–	Westgate et al. (1989)

new organs during the period of stress recovery (Calvache et al. 1997). Plants with a perennial growth habit and deep rooting characteristics are better able to withstand drought than shallow-rooted annuals (Farooq et al. 2009).

Solute accumulation

Accumulation of compatible solutes is an important strategy for osmotic adjustment and osmoprotection during drought. Compatible solutes primarily accumulate in the cytosol of stressed cells without interfering with the macromolecules and are either: (i) nitrogen-containing compounds such as proline or other amino acids, quaternary ammonium compounds and polyamines (Rontein et al. 2002), or (ii) hydroxyl compounds such as sucrose, polyhydric alcohols and oligosaccharides. The mechanism of osmoprotection is based on the intimate association of non-toxic compounds with various cellular components whereas osmotic adjustment helps in turgor maintenance by adjusting the water content in cells and tissues (Chen and Murata 2002). If the accumulation of osmolytes is sufficient to decrease cell osmotic potential, the cell will maintain water absorption and cell turgor at lower water potentials (Morgan 1984, Farooq et al. 2009).

Proline plays a major role as an osmoticum due to its zwitterionic, high hydrophilic characteristics; it has compatible actions in the cell cytoplasm without interfering with cellular structure and metabolism. During drought, proline – acting as a signalling molecule – can modulate mitochondrial function and influence cell proliferation and cell death by triggering specific genes, which otherwise are

essential for a particular plant to recover from stress (Szabados and Saviouré 2009). Accumulation of proline helps to maintain membrane integrity by reducing lipid oxidation through scavenging free radicals and protecting cellular redox potential (Ashraf and Foolad 2007).

Among compatible solutes, sugars especially the non-reducing di-, tri- and tetrasaccharides help to maintain membrane integrity (Ramanjulu and Bartels 2002). Mannitol, the most widely distributed sugar alcohol in nature (Stoop et al. 1996), helps scavenging hydroxyl radicals and stabilizes macromolecular structures such as phosphoribulokinase, thioredoxin, ferredoxin and glutathione (Shen et al. 1997). Trehalose, a non-reducing disaccharide, modulates the stabilization of biological structures and macromolecules (protein, membrane lipids) thereby helping to maintain photosynthesis under stress (Crowe et al. 1992). The protective effect seems to result from the creation of hydrogen bonds between macromolecules and osmolytes thus preventing formation of intramolecular H-bonds that could otherwise irreversibly modify the three-dimensional molecular structure. In grain legumes, increased sugar alcohol (e.g. sorbitol and inositol) with concomitant decrease in sugar is a major osmoticum during drought (Amede and Schubert 2003).

Antioxidant defence

Production of ROS is an early plant response to drought and acts as a secondary messenger to trigger subsequent defence reactions in plants (Farooq et al. 2009). During drought, ROS such as superoxide anion (O_2^-), H_2O_2 ,

hydroxyl (OH), alkoxy radicals (RO) and singlet oxygen ($^1\text{O}_2$) are generated and accumulated (McCord 2000), which injure cellular structures and macromolecules (Smirnov 1993). ROS play two divergent roles in plants depending on the delicate equilibrium between production and their scavenging. Acting as a signalling molecule at lower concentrations, ROS mediate several responses in plant cells in a low water environment. When the concentration exceeds the defence mechanism, ROS cause oxidative damage to lipids, proteins, nucleic acids and hereditary material (like DNA) leading to altered intrinsic properties of biomolecules and cell death (Foyer 2005).

The antioxidant defence system of these ROS inside the cell is governed by both enzymatic and non-enzymatic components. Maintaining high levels of antioxidant or inducing antioxidant enzymes are proven adaptive mechanisms during drought (Farooq *et al.* 2009). Enzymatic antioxidants include superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione peroxidase (GPX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR) and glutathione reductase (GR) (Farooq *et al.* 2009). On the other hand, ascorbate, glutathione, carotenoids, tocopherols, ascorbic acid and phenolics serve as potent non-enzymatic antioxidants inside cells (Farooq *et al.* 2009).

Of the enzymatic antioxidants, SOD acts as a first line of defence via detoxification of superoxide radicals and hydrogen peroxide (H_2O_2) to water and molecular oxygen thereby preventing oxidative damage (Noctor *et al.* 2000). APX – a key enzyme in the glutathione ascorbate pathway – helps to regenerate NADP^+ and converts H_2O_2 to water (Jiménez *et al.* 1998). Hydrogen peroxide is removed by APX where GR and DHAR help by providing a substrate for the reaction. Studies on oxidative stress showed that these antioxidants or their transcripts (e.g. GR or APX) may be higher during the recovery than during the stress period, as observed in pea (Mittler and Zilinskas 1994). During drought, higher increments in the activities of SOD, GR, APX, GPX, GST and POD were also recorded in resistant varieties of horse gram (*Macrotyloma uniflorum* (Lam.) Verdc.) and common bean (Saglam *et al.* 2011, Bhardwaj and Yadav 2012). Therefore, the estimation of specific antioxidant enzyme activities and/or expression analysis is considered important for assessing the involvement of the scavenging system to protect the plant from toxic effects of ROS during drought.

Stay green and remobilization of stem reserves

Stay green is a term given to a genotype where leaf senescence is delayed when compared with a standard reference genotype and is regarded as a vital characteristic associated with the ability of a plant to maintain CO_2 assimilation and

carry out photosynthesis. Stay green has two types: (i) functional stay green where maintenance of chlorophyll and photosynthetic competence is present, and (ii) non-functional stay green where chlorophyll is maintained, but other components of the photosynthetic apparatus are degraded. For instance, shading a plant often extends the green area duration of its mature leaves (Mae *et al.* 1993).

Muchero *et al.* (2013) demonstrated a close association of expression of the stay-green trait with grain and biomass yield of cowpea under drought stress. In contrast, Kumudini (2002) and Ismail *et al.* (2000) reported that, under field conditions, the functional stay-green trait can be of limited or even negative value for N-dominating yield of grain legumes such as soyabean and cowpea due to the use of N for maintenance of functional stay green. The stay-green characteristic of grain legumes could potentially increase pod yield through prolonged photosynthesis during pod filling (Ronghua *et al.* 2006). Hence, delaying leaf senescence may be particularly advantageous under drought to extend the duration of active photosynthesis and to maintain the supply of assimilated carbon to developing grain during grain filling in legumes.

Reproductive success under terminal drought is also associated with the ability of the plant to store reserves in vegetative organs (stems and roots) for later remobilization for grain development (Davies *et al.* 2000, Chaves *et al.* 2002). However, the potential for storing reserves in the stem depends on stem length and weight density; whereas remobilization ability depends on sink size (Davies *et al.* 2000, Farooq *et al.* 2009). Interestingly, the stem (stem stele in particular) is well protected against water deficit. In lupin for instance, the relative water contents (RWC) of stem stele never dropped below 83 %, whereas other organs had RWCs below 60 % (Pinheiro *et al.* 2004). However, staying green for too long may result in non-remobilization of pre-anthesis reserves in leaves, glumes and stems (Gebbing and Schnyder 1999).

Hormonal regulation

Phytohormones namely auxins, gibberellins, cytokinins, ABA, ethylene and jasmonates are involved in drought resistance. Phytohormones have both synergistic and antagonistic interactions. For example, the increase in cytokinin concentration under drought in plant xylem sap promotes stomatal opening by decreasing its sensitivity to ABA (Wilkinson and Davies 2002). The endogenous concentration of auxin, gibberellin and cytokinins decreases during drought while ABA and ethylene tend to increase in almost all plants (Weyers and Paterson 2001).

An increase in ABA concentration during drought is due to a reduction in ABA catabolism preventing its symplastic entry from both rhizosphere and phloem. Increased xylem

pH (alkalinization) during drought also promotes ABA loading to root xylem (Hartung et al. 2002). For instance, in kidney bean (*Phaseolus vulgaris* L.), reduced stomatal conductance was associated with an increase in ABA accumulation promoted by rewatering (Miyashita et al. 2005). ABA promotes root hydraulic conductivity which is responsible for ease of water uptake and transport within the plant. ABA also increased the production of O_2^- radicals and H_2O_2 , enhancing the activities of antioxidant enzymes such as GR. Therefore, overexpression of the ABA synthesis gene can serve as a hope to combat drought.

Improving Terminal Drought Resistance

To increase the productivity of grain legumes, concurrent development of drought-resistant genotypes and strategies for efficient water management are important. Thus to improve and sustain the productivity of grain legumes under drought, drought-resistant genotypes and a site-specific package for production technology are desired. Focusing on functional genomics and biotechnology to improve drought resistance is gaining momentum; however, this may cause a phenotype gap (Farooq et al. 2014). Hence integrated use of modern tools with conventional breeding protocols may yield more benefits. This section discusses the selection, breeding, molecular and transgenic approaches used to improve drought resistance in grain legumes.

Selection and breeding

Improving resistance against terminal drought in crop species through conventional breeding is a proven strategy and is expected to remain the principal method for crop improvement (Farooq et al. 2014). However, the selection and breeding process requires substantial heritable variation to improve drought resistance in grain legumes (Frahm et al. 2004, Beebe et al. 2008). Nonetheless, breeding progress is often hindered by the quantitative genetic basis of the trait and the incomplete understanding of the physiological basis of yield crop response in water-limited conditions (Torres et al. 2010). Furthermore, heritability is often low due to variations in the timing and amount of precipitation received, and high genotype and environment interactions in dry environments. Despite this, it is important to identify relevant traits that confer yield stability and/or potential under terminal drought stress. In addition, good characterization of the environment is a prerequisite to enhance the usefulness of any given trait of interest (Mir et al. 2012).

Screening and mass selection may be useful to obtain desirable phenotypic characteristics based on the traits strongly correlated with yield.

However, quite often it is cumbersome to accurately phenotype crop plants for a target trait as most of the physiological traits with strong association with terminal drought require sophisticated techniques, and can only be applied to small group of genotypes. Therefore, the first tier of selection may be based on simple, rapid and easy-to-measure traits. This may be followed by more precise screenings of less number of genotypes in the second tier. Mass selection should, therefore, be based on heritable traits that are economical and relatively easy to measure, and do not result in penalties under favourable conditions, nor be associated with negative pleiotropic effects on other important agronomic traits (Farooq et al. 2014).

In crops such as chickpea, common bean, soyabean and cowpea, certain root traits such as root length, density, rooting depth and a fibrous root system are promising for terminal drought avoidance (Khan et al. 2010, Hall 2012, Duc et al. 2015), and may be used for screening grain legume genotypes for drought resistance. However, some recent studies (Zaman-Allah et al. 2011a,b) have reported that selection for yield under terminal drought conditions was not essentially dependent on root systems, but rather on several other critical traits including: (i) low leaf conductance under non-limited water conditions during the vegetative stage, (ii) low leaf expansion rate when soil moisture is non-limiting for plant growth and when plant growth is restricted under progressive exposure to stress, and (iii) a higher fraction of transpirable soil water (FTSW) thresholds that reduce transpiration, thus avoiding rapid soil water depletion. Traits such as early flowering, podding and maturity provide an escape mechanism, and may be used for mass screening (Duc et al. 2015). Higher stomatal conductance and cooler canopies have often been associated with higher grain yield under terminal drought and these traits may provide indirect selection criteria (Duc et al. 2015).

Canopy spectral reflectance is an effective non-invasive high-throughput phenotyping technique (Montes et al. 2007, Chapman 2008), enabling easy and quick measurements of several dynamic complex traits including plant canopy size, carbon assimilation and biomass accumulation (Montes et al. 2007). Canopy spectral reflectance may, therefore, be used for mass screening of grain legume genotypes for drought resistance. Thermal infrared imaging (also called infrared thermography), which estimates leaf or canopy temperature, may also be employed to screen grain legumes for drought resistance. Plant canopy temperature is a widely measured variable that is closely related to canopy conductance at the vegetative stage (Zaman-Allah et al. 2011a) and therefore provides insight into plant water status. Thermal infrared imaging for estimating conductance can be used at the whole plant or canopy level over time.

Table 3 Drought-resistant genotypes of grain legumes developed through conventional breeding

Crop species	How developed?	Institutes involved	References
Chickpea	Line-source	ICRISAT	Saxena (1987)
	Drought-susceptibility index (DSI)	ICRISAT	Saxena (1987)
Common bean	Recurrent selection	CIAT	Beebe et al. (2008)
	Advanced backcrossing	CIAT	Blair et al. (2006)
	Double cross	CIAT	Miklas et al. (2006)
	Congruity backcrossing	Department of Horticultural Science and Landscape Agriculture, USA	Haghighi and Ascher (1988)
Faba bean	Cytoplasmic genetic male sterility (CGMS)	Departamento de Genética, Instituto de Biotecnologia, Universidade Federal do Rio Grande do Sul, Brazil	Homrich et al. (2012)
Pigeonpea	DSI	ICRISAT	Chauhan et al. (1998)
Tepary beans (<i>Phaseolus acutifolius</i>)	Congruity backcrossing	Department of Horticulture Science and Landscape Agriculture, US	Haghighi and Ascher (1988)

CIAT, International Center for Tropical Agriculture; ICRISAT, International Crops Research Institute for the Semi-Arid Tropics.

Assessments of delayed senescence may be useful for indirect selection of grain and biomass yields in breeding programmes targeting improved drought resistance (Muchero et al. 2013). Furthermore, key physiological attributes including leaf water potential index (Karamanos and Papatheohari 1999), water use (Amede et al. 1999), leaf temperature and carbon isotope discrimination ($\Delta^{13}\text{C}$) (Khan et al. 2010), and may be useful in screening grain legume genotypes for drought resistance. There exists substantial genetic diversity in chickpea genotypes for carbon isotope discrimination (Krishnamurthy et al. 2013). Therefore, ^{13}C may also be used for root system improvements in chickpea as an indirect indicator.

Wide hybridization is another strategy employed in breeding to achieve a desirable trait within or between species. Interspecific crosses have been undertaken in many grain legumes with variable success (Chowdhury and Chowdhury 1977). There is great scope for using this strategy in breeding programmes aimed at improving drought resistance in grain legumes (Table 3). In this context, *Phaseolus vulgaris* can be cited with its wild relative *Phaseolus acutifolius*, which has higher osmotic adjustment than the former, hence necessitating its transfer to cultivated beans with the help of interspecific hybridization (Parsons and Howe 1984). However, osmotic adjustment may have poor stability depending upon the stress level, location or physiological stage of the plant (Basu et al. 2007).

Promising germplasm accessions have been developed in various grain legumes in drought-related backgrounds, some of which have been found in chickpea (e.g. ICC 4958) and related to root length density, root depth, canopy temperature, terminal drought, etc. Similar success stories have been reported in chickpea cultivars when wild genes were transferred from *C. reticulatum* to cultivated chickpea resulting in nine genotypes well adapted to water stress (Kashiwagi et al. 2005).

Quantitative trait loci for drought resistance

Molecular and genome-based approaches are quite helpful in identifying and accessing desirable alleles, present at different quantitative trait loci (QTL), with the potential to affect desired responses (Farooq et al. 2014).

Morpho-physiological traits, affecting the drought resistance mechanism, are quantitatively inherited. Therefore, discovery of QTL plays a central role in crop improvement through marker-assisted selection (MAS). There are several breeding strategies involved in the improvement of drought resistance in grain legumes based on MAS. The MAS strategy uses molecular markers to separate QTL by mapping, a prior necessity to MAS. Markers are often associated with MAS to lessen linkage drag associated with undesirable alleles linked to target genes. Nowadays, PCR-based markers have replaced older generation markers such as RFLP (restriction fragment length polymorphism) increasing the cost effectiveness of MAS. Marker-assisted pyramiding is part of MAS, which combines several genes into a single genotype (Witcombe et al. 2008). To reduce linkage drag in gene pools, various backcrossing methods have been established. Marker-assisted backcrossing selection (MABS) is one such strategy where QTL with higher phenotypic variation are separated and termed major QTL. After validation, they can be introgressed into low drought-resistant genotypes without transferring the undesirable gene. This process gives superior lines with improved drought resistance (Varshney and Dubey 2009, Gupta et al. 2010). Similarly, marker-assisted recurrent selection (MARS) is used when multiple QTL control a particular trait. It is used to introgress selected traits in every cycle with F_2 populations mostly used to increase the frequency of favourable alleles (Eathington et al. 2007).

In cowpea, 12 QTL associated with seedling drought resistance and maturity have been reported (Table 4).

Correspondingly, Muchero et al. (2009) reported 306 AFLP markers from cowpea, which were later used for genetic mapping. Seven markers – namely ACC-3, CPRD8-1, CPRD14-2, CPRD14-3, CPRD22-2, CPRD22-4 and VuPAT1-2 – were correlated with QTL *Dro-5*, *Dro-5*, *Dro-3*, *Dro-1*, *Dro-2*, *Dro-4* and *Dro-3*, respectively. QTL related to WUE and LASH (leaf ash) under terminal drought conditions in soyabean were also identified and, for this particular perspective, Mian et al. (1996) developed an RFLP map considering 120 F₄-derived lines of a soyabean population generated from a cross of ‘Young × PI416937’. In addition to significant phenotypic changes observed for both traits, four and six RFLP markers were detected in the lines for WUE and LASH, respectively. A major QTL *cr497-1* related to WUE was also reported, showing a variation of 13.2 % on USDA linkage group (LG) J. Two QTLs for both WUE and LASH were also observed, maintaining the gap to be filled in identifying the QTL affecting root

architecture, an essential trait for adapting to water deficit (Manavalan 2009).

OMICS-based approaches

OMICS is a technology used to identify candidate genes responsible for a specific trait and to define their specific function. It mainly uses transcriptomics (RNA), proteomics (protein) and metabolomics (metabolite) to locate candidate genes thereby assisting QTL mapping. Phenomics, another OMICS technology, aims to identify the candidate or possible surrogate gene responsible for a trait. With the advent of new generation sequencing (NGS) platforms, several studies have reported transcriptome-based sequencing of legume crops. NGS-based approaches are being used to a genome-scale survey of sRNAs (Joshi et al. 2011, Song et al. 2011). In soyabean for instance, transcriptome atlas has been developed to perform RNA sequences of samples from 14 distinct water-stressed conditions using an NGS platform (Libault et al. 2010). Studies in soyabean proteomics revealed the presence of 35 proteins in drought-stressed roots. Proteins such as ferritin, which provide protection from oxidative stresses (Strozycki et al. 2007), showed upregulation in drought-treated roots rather than the respective controls (Yamaguchi et al. 2010).

Similar experiments in chickpea related to root traits and drought resistance identified 106 expressed sequence tags (EST)-based markers, SSR markers and unitags through SUPERSAGE analysis which bring new opportunities for chickpea research (Jayashree et al. 2005). The generated set of chickpea ESTs serves as a resource of high quality transcripts for gene discovery and development of functional markers associated with drought resistance and may help facilitate breeding grain legumes for drought resistance (Varshney et al. 2009). In chickpea, some dehydration-responsive proteins were identified revealing their functions in cell wall modification and signal transduction under drought (Pandey et al. 2008). Studies on the chickpea nucleus, exposed to drought to examine the metabolic network, were fed 205 differentially regulated protein spots and 147 differentially expressed proteins, and found to be involved in protein degradation, nucleocytoplasmic transport, gene transcription and replication, molecular chaperones, ROS pathway, cell signalling and chromatin remodelling (Pandey et al. 2008). This dehydration-responsive regulatory network is directed by the production of certain proteins such as Ran (CaN-347), a *Ras*-related protein strongly upregulated under drought (Melchior and Gerace 1998). Similarly, some LEA proteins called dehydrins (CaN-600) were produced under stress thereby protecting enzyme activity by scavenging ROS (Close 1996).

Table 4 QTL identified from various grain legumes with their respective traits

Crop	Character	QTL	Linkage group	References
Chickpea	Grain weight	<i>Qncl.Sw1</i>	LG1	Radhika et al. (2007)
		NCPGR-50	3	Hamwiah et al. (2013)
		TR-50	3	
		SCEA19	7	
		TAA-58		
	Grain yield	H6C-07	3	Hamwiah et al. (2013)
		H5E-02	U	
		H5G-01	4	
		H6C-07	3	
		H1B-04	3	
	Harvest index	TA-113	U	Hamwiah et al. (2013)
		TR-58	2	
		H6C-07	3	
H1F-21		5		
Drought resistance score	H6C-07	3	Hamwiah et al. (2013)	
Cowpea	Drought-induced senescence	<i>Dro-1</i>	LG 1	Muchero et al. (2009)
		<i>Dro-2</i>		
	Maturity	<i>Mat-1</i>	LG 7	Muchero et al. (2009)
		<i>Mat-2</i>	LG 8	
Pigeonpea	Fertility restoration	QTL-RF-1	–	Saxena et al. (2011)
		QTL-RF-2		
		QTL-RF-3		
		QTL-RF-4		
Soyabean	Enhanced fibrous root	Q_root_Gm01	Gm01	Abdel-Haleem et al. (2011)
		Q_root_Gm03	Gm03	
		Q_root_Gm04	Gm04	
		Q_root_Gm08	Gm08	

Transgenic approaches

Candidate-gene-based transgenic technology has emerged as a useful approach for understanding mechanisms of resistance against drought, which is expected to provide a complementary way for genetic improvement of crop plants. Recent developments in biotechnology have made it possible to identify drought-responsive genes from species other than target plants and to tailor transgenic grain legume plants resistant to terminal drought. Transgenic legumes can be developed by transfer through biolistics or *Agrobacterium*-mediated transformation. The ideal candidate gene should improve drought resistance without yield penalty when introduced into various genomes. Several attempts are underway and reported in different legumes where transgenic drought-resistant crops are developed using genes isolated from legumes as well as other crop species.

Genetically engineered drought-resistant legume plants using single-gene products, which encoding enzymes involved in the modification of membrane lipids (Kodama et al. 1994), late embryogenesis proteins and biosynthesis of osmoprotectants (Kavikishore et al. 1995) have been developed (Table 5). The whole process depends on factors

such as extent of drought, the ability to transfer the resistance mechanism and the effect on biomass and yield (Mathur et al. 2009).

An osmoregulatory gene *P5CSF129A* encoding the mutagenized D1-pyrroline-5-carboxylate synthetase (P5CS) was introduced into a chickpea genotype, which increased the proline biosynthesis manifold with a simultaneous reduction in free radicals and malonaldehyde levels, but no significant increase in biomass accumulation. However, transpiration efficiency was substantially improved (Mathur et al. 2009).

Genes belonging to the AP2/ERF (APETALA2/ethylene response factor) family, an important family of plant transcriptional regulators, and DREB (dehydration-responsive element-binding) transcription factors play a crucial role in plant development and in response to various stresses. Anbazhagan et al. (2014) engineered drought-tolerant transgenic chickpea through *Agrobacterium*-mediated transformation by overexpressing *DREB1A* driven by the Arabidopsis *rd29A* promoter under drought where all transgenic events increased *DREB1A* gene expression before 50 % of soil moisture was lost. The results indicated the efficacy of *rd29A : DREB1A* on mechanisms underlying water uptake, stomatal response, transpiration efficiency

Table 5 Candidate genes implored for imparting drought resistance isolated from various grain legumes

Crop	Candidate gene	Action/mechanism	References
Broad bean	VfPIP1	Aquaporin/water transport	Cui et al. (2008)
Chickpea	DREB2A	Transcription factors	Nayak et al. (2009)
	AP2/ERF, MyB, XPB1	Transcription factors	Deokar et al. (2011)
	Zinc finger family, MYB domain containing family, WRKY, auxin response factor, pentatricopeptide-repeat-containing protein, bZIP	Transcription factors	Hiremath et al. (2011)
Common bean	DREB2B	Non-ABA dependent responses	Cortés et al. (2012)
	PvLEA3	Protein stabilization	Barrera-Figueroa et al. (2007)
	Aquaporin	Water allocation	Montalvo-Hernández et al. (2008)
	Asr1 Asr2	ABA signalling pathway	Cortés et al. (2012)
Cowpea	CPRD8, CPRD12, CPRD14, CPRD22, CPRD46 phospholipase D, VuPLD1, 9-cis-epoxycarotenoid dioxygenase, VuNCED1	ABA biosynthesis	Muchero et al. (2010)
Pigeonpea	CcM1522–CcM1821, CcM0047–CcM2332		Saxena et al. (2011)
	MyB, WRKY, NF-Y	Transcription factors	Yang et al. (2006)
Soyabean	GmDREB, GmNAC, GmZIP, ERF089	Transcription factors	Manavalan (2009)
	<i>rd29A : DREB1A</i>	Transcription factors	Bhatnagar-Mathur et al. (2007)
	GmCaM4	Up regulates several drought-responsive genes	Yoo et al. (2005)
	CDPK	Phosphorylates aquaporin thereby enhancing water permeability across membranes	Guenther et al. (2003)
	Histidine kinases (GmHK) and receptor-like protein kinases (GmCLV1A, GmCLV1B, GmRLK1, GmRLK2, GmRLK3 and GmRLK4)	Osmosensors	Yamamoto et al. (2000)

and rooting architecture in water-stressed plants thereby imparting drought resistance compared with untransformed controls.

Soyabean drought-tolerant transgenic plants have been developed by Li et al. (2013), which overexpress the Arabidopsis *LOS5/ABA3* gene, which encodes molybdenum cofactor sulphurase involved in aldehyde oxidase (AO) activity and regulates ABA biosynthesis indirectly under the control of a constitutive super promoter. Overexpression of *LOS5/ABA3* enhanced AO activity, ABA accumulation and expression of stress upregulated genes, leading to 21 % more seed yield in transgenic than the wild-type plants under field drought conditions.

Cowpea clones responsive to dehydration were designed using 12 candidate genes namely 9-cis-epoxycarotenoid dioxygenase, *VuNCED1* (Iuchi et al. 2000), phospholipase D, *VuPLD1* (El-Maarouf et al. 1999), patatin-like galactolipid acyl hydrolase, *VuPAT1* (Matos et al. 2001), phosphatidylinositol-specific phospholipase C, *VuPI-PLC* (El-Maarouf et al. 2001), *CPRD8*, *CPRD12*, *CPRD14*, *CPRD22*, *CPRD46* (Iuchi et al. 1996), ascorbate peroxidase, *VuAPX* (D'Arcy-Lameta et al. 2006) and multicystatin, *VuC* (Diop et al. 2004). The *VuNCED1* gene played a crucial role in catalysing a key step in ABA synthesis. In drought-stressed plants, *VuNCED1* expression and ABA level was higher than in control plants while the ABA level was reportedly 160 times more than controls. Similarly, *VuPLD1* was responsible for drought-induced membrane phospholipid degradation. It was expressed in susceptible cultivars and remained unchanged in tolerant cultivars suggesting that drought-tolerant plants have their own machinery for regulating enzymes responsible for membrane phospholipid degradation.

Nonetheless, none of the drought-resistant transgenic plants are commercially grown. Blum (2014) opined that 'insufficient phenotyping of experimental transgenic plants for drought resistance often does not allow true conclusions about the real function of the discovered genes towards drought resistance'.

Management Practices

Management practices such as adjustment of sowing time and geometry, and application of fertilizers and micronutrients can help plants to improve their resistance capacity against drought (Siddique et al. 2012). The major impact of management practices on rainfall use efficiency is to increase the total crop water use via transpiration and to reduce the water loss by weeds and/or soil evapotranspiration. While chemical constraints to root growth are difficult to remediate, subsoil compactness may be removed by gypsum application, which helps flocculating the soil particles to improve water infiltration and root growth (Hamza

and Anderson 2003). In this regard, selection of appropriate cultivars is also very important.

Planting time and geometry

Adjusting the sowing or planting time can influence critical crop growth stages such as flowering time and pod filling and thus reduce the adverse effects of drought during these stages (Kumar et al. 2008). Early planting with increased plant density can be beneficial as it provides higher water use or rainfall use efficiency for better yields (Turner 2004). Grain legumes can be successfully cultivated in drought-prone areas by matching critical crop growth stages with the period of water availability to minimize yield losses. Planting geometry plays a major role in the yield performance of crops. Maintaining a preferred/optimum planting density is essential for natural resource use such as light, water, nutrients and space. Under rainfed conditions, high plant density will deplete soil moisture before maturity and more water will be lost through transpiration, whereas lower plant density will leave soil moisture unused. Some researchers have observed that lower planting densities result in lower yields due to more 'pinched grains' particularly in Mediterranean-type environments (O'Connell et al. 2004). Therefore, optimum planting densities are beneficial for higher rainfall use efficiency and to obtain maximum yields per unit area.

Nutrient management

Management of macro- and micronutrients is effective for developing drought resistance in plants as better plant nutrition can effectively alleviate the adverse effects of drought (Waraich et al. 2011). Fertilizer application has a marked beneficial effect on rainfall use efficiency and hence crop yield. Both nitrogen and phosphorus nutrition can increase crop water use, thereby reducing soil evaporation. For instance, P fertilizers increased stomatal conductance, photosynthesis, membrane stability, leaf water potential and root growth during drought to improve osmotic adjustment in beans and sorghum (Alkaraki et al. 1996). Sufficient K supply corrects the drought-induced reduction in photosynthesis in grain legumes by maintaining higher tissue water potential (Sangakkara et al. 2000). Application of N increased yield, yield attributes and protein concentration in chickpea (Palta et al. 2005). In soyabean application of farmyard manure in combination with inorganic fertilizers improved the soil organic carbon contents; grain yield and WUE were also improved by 103 % and 76 %, respectively, than control (Hati et al. 2006). Legume yields can be significantly improved by applying timely irrigation particularly at critical growth stages, which can reduce pod abortion (Leport et al. 2006).

Selenium (Se) helps to increase the water uptake capability of the root system under drought (Farooq et al. 2014). Application of Se to drought-stressed soyabean and chickpea plants reduced the level of lipid peroxidation and increased the activity of certain antioxidant enzymes such as SOD and GPX; that is, it acted as a putative antioxidant (Mohammadi et al. 2011). Grams et al. (2007) reported that Se can delay leaf senescence and promote growth of ageing seedlings.

The addition of silicon (Si) significantly increased RWC in drought-stressed plants (osmotic adjustment) by increasing the concentration of proline and glycine betaine (Hattori et al. 2005). It has also improved the plasma membrane and tonoplast structure in terms of function and integrity, and chlorophyll fluorescence under drought (Silva et al. 2012). The beneficial effects of Si may result from better and more efficient osmoregulation, reduced transpirational water loss, maintenance of adequate supply of essential nutrients, controlled toxic ion uptake and efficient functioning of antioxidative mechanisms thereby modulating a plant's metabolism (Sacala 2009). Si nutrition promotes nodule formation for efficient nitrogen fixation in cowpea plants (Mali and Aery 2008). Sole application of Si or combined with K significantly increased shoot dry matter yield in drought-stressed plants of chickpea (Kurdali et al. 2013).

Zinc (Zn) is one of the essential micronutrients, which is a metal, functional, and structural component or cofactor of several key enzymes (Marschner 1986). Shaban et al. (2012) reported significant increases in grain and biomass yields in chickpea with application of Zn fertilizer. Foliage applied zinc sulphate improved the growth, yield and related traits of mungbean under drought (Thalooth et al. 2006). While examining common bean cultivars grown under water-limited conditions, Yadavi et al. (2014) concluded that Zn and iron (Fe) application can ameliorate the impact of drought by increasing RWC and has a positive impact on protein and micronutrient contents of grain. Boron is another vital micronutrient required for nodule development and nitrogen fixation. Foliar application of boron improved the nodule growth, in terms of number and mass, in soyabean under drought (Yamagishi and Yamamoto 1994).

Inoculation with arbuscular mycorrhizal fungi and rhizobacteria

Arbuscular mycorrhizal fungi (AMF) associated with plant roots form common mycorrhizal network (CMN) within and between plant roots may enhance crop productivity under water deficit conditions owing to increased uptake and transport of water and nutrients especially N and P (Augé 2001). Because of the entrapment of soil particles by

hyphae, AMF can improve soil water retention properties through formation and stabilization of soil aggregates. Glomalin, a glycoprotein produced by AMF, helps to improve soil structure (Smith et al. 2010). The extraradical mycelium produced by AMF can extend and explore a great volume of soil which helps in the uptake of more water from soil. Thus, AMF assist in the maintenance of tissue water status, an avoidance mechanism to mitigate the adversities of drought on plant growth (Porcel and Ruiz-Lozano 2004, Habibzadeh 2015). Furthermore, AMF inoculation can improve drought resistance by increasing antioxidant potential, decreasing lipid peroxidation (Porcel et al. 2003, Sohrabi et al. 2012) and increasing osmoprotectants (Porcel and Ruiz-Lozano 2004, Habibzadeh 2015), which ultimately increase grain yield (Habibzadeh 2015). Atimanav and Adholeya (2002) reported increased growth rates and phosphate uptake in legumes with AMF application.

Plant growth promoting rhizobacteria (PGPR) help to improve plant growth and productivity under optimum and stress conditions via direct and indirect mechanisms (Glick et al. 2007, Nadeem et al. 2010) such as phosphorus solubilization, nitrogen fixation, production of siderophores, plant growth promoting substances and organic acids as well as protection by enzymes such as ACC deaminase, chitinase and glucanase (Glick et al. 2007, Hayat et al. 2010) (Table 6). PGPR can produce and/or metabolize the main phytohormone classes – auxins, gibberellins, cytokinins, ethylene and ABA (Dimkpa et al. 2009). Application of PGPR can alleviate the damaging effects of drought stress to improve crop yields (Dodd 2009). Most rhizobacteria (RBs), which promote growth and developmental cascades of crop plants, produce indole acetic acid (IAA) which promotes cell elongation with concomitant increase in root growth. Inoculation of different plant species with RBs improved lateral root and root hair development, thereby increasing root surface area, and thus helping to improve nutrient and water uptake (Dimkpa et al. 2009). Bacterial hydrolysis of ACC (1-aminocyclopropane-1-carboxylic acid) suppresses ethylene production in plants thereby promoting root growth (Long et al. 2008). Rhizobacteria like *Arthrobacter*, *Burkholderia* and *Bacillus* also trigger proline biosynthesis in plants under less than optimum conditions (Barka et al. 2006, Sziderics et al. 2007). Proton efflux activities in cowpea and soyabean roots were positively and significantly affected by inoculation with *Azospirillum* (Bashan et al. 1992). Belimov et al. (2009) observed hormone-signalling-mediated improvements in plant growth, yield and WUE in droughted pea plants upon inoculation with ACC-deaminase activity containing *Variovorax paradoxus*. Due to the activity of ACC deaminase, RBs can convert ACC into ammonia and α -ketobutyrate, thereby protecting plants from deleterious concentrations of ethylene (Nadeem et al. 2014).

Table 6 Influence of arbuscular mycorrhizal fungi and rhizobacteria on drought resistance in grain legumes

Bacterial/AMF strain	Crop species	Plant response	References
<i>Bacillus</i> spp.	Common bean	Root hair proliferation and enhanced nodulation	Srinivasan et al. (1996)
<i>Glomus intraradices</i>	Common bean	Maintained stomatal conductance	Augé (2004)
<i>Gigaspora margarita</i>	Common bean	Dehydration maintenance	Augé (2004)
<i>Paenibacillus polymyxa</i> + <i>Rhizobium tropici</i>	Common bean	Improved plant growth, nitrogen content and nodulation	Figueiredo et al. (2008)
<i>Glomus intraradices</i>	Common bean	Maintained root hydraulic conductance	Aroca et al. (2007)
<i>Azospirillum brasilense</i>	Common bean	Root growth	German et al. (2000)
<i>Azospirillum</i> spp.	Cowpea	Positive impact on proton efflux activities	Bashan et al. (1992)
<i>Glomus intraradices</i>	Cow pea	Maintained stomatal conductance	Augé et al. (1992)
<i>Glomus mosseae</i>	Green gram	Increased water-use efficiency	Yagoob et al. (2013)
<i>Glomus intraradices</i>	Green gram	ACC-deaminase production, root growth	Mayak et al. (1999)
<i>Pseudomonas putida</i>	Lentil	Improved growth and nodulation	Chanway et al. (1989)
<i>Pseudomonas putida</i>	Pea	Hormone-signalling-mediated plant growth improvement, yield and water-use efficiency	Belimov et al. (2009)
<i>Pseudomonas</i> spp.	Pea	No effect on growth of pea	Chanway et al. (1989)
<i>Bacillus</i> spp.	Soyabean	Increased pod formation, nodulation	Li and Alexander (1988)
<i>Pseudomonas</i> spp.	Soyabean	Maintained higher leaf water potential	Aliasgharzad et al. (2006)
<i>Glomus mosseae</i>	Soyabean	Maintained stomatal conductance	Augé et al. (1992)
<i>Glomus etunicatum</i>	Soyabean	Root osmotic adjustment protected against oxidative stress	Porcel and Ruiz-Lozano (2004)
<i>Pseudomonas cepacia</i>	Soyabean	ACC-deaminase production, early growth	Cattelan et al. (1999)
<i>Bradyrhizobium japonicum</i>	Soyabean	Enhanced N content	Aliasgharzad et al. (2006)

It is evident from the literature that AMF and PGPR can promote plant growth and productivity even under soil water deficiency by regulating nutritional and hormonal balances, producing plant growth regulators and solubilizing essential plant nutrients. Besides the beneficial effects of sole application of AMF and PGPR, their combined applications have reportedly been equally effective for drought resistance. For instance, Figueiredo et al. (2008) assessed the effect of inoculation with *Rhizobium tropici* and *Paenibacillus polymyxa* on nodulation, growth and nitrogen assimilation in common bean under drought. Inoculation improved nodulation, growth and nitrogen assimilation under drought compared with the uninoculated control.

Conclusion and Future Research

In regions with frequent episodes of terminal drought, selection and development of appropriate cultivars may help to reduce the duration of stress exposure. Early season planting and early vigour help to reduce soil water loss; in early season planting, the time to flowering and grain filling may shorten, which helps to minimize the effects of terminal drought. Adoption of conservation agriculture in legume-based cropping systems may help to minimize terminal-drought-induced yield losses. While the effects of drought stress on grain legumes are relatively well under-

stood, further research on the physiological mechanisms of drought resistance through drought escape, phytohormonal regulations, stay-green characteristics and management practices under field conditions is needed. Scavenging ROS through modulation of antioxidant systems, phytohormonal regulations, stability of biological membrane and accumulation of compatible solutes are vital mechanisms of drought resistance to ensure satisfactory economic yields under terminal drought. This can be achieved by adopting better gene pool management along with suitable agronomic practices to enable plants to restore yield. As crop productivity is mainly determined by its photosynthetic activity, the stay-green characteristic in grain legumes is important to combat terminal drought. Inhibition of both N partitioning and fixation under water-limited environments reduces protein accumulation in seeds which reduces grain quality in legumes. Hence, it is essential to combine crop physiology with molecular biology to further improve terminal drought resistance in grain legumes. As discussed above, MAS has been highly developed with the introduction of various RFLP markers replacing older ones, but it needs fine-tuning to be effective when combining favourable alleles and removing undesirables. Development of transgenics, which are tolerant to multiple stress environments, is gaining pace but needs more focus. Many candidate genes responsible for

resistance against terminal drought in grain legumes have been identified. Further research on their wild relatives and other landraces would identify more candidate genes to contribute to drought resistance studies.

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