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Drought mitigation strategies in pulses

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Abstract

Pulses are very crucial in human diet as it is a potent source for protein. These also play significant roles in conservation farming systems and add to food security in the developing countries. Climate change in particular with drought is one of the most important reasons for the adverse effect on its area production and productivity in many regions of the world. The amount of water reduction is directly proportional with yield reduction, but the degree of the impact varies with legume species and the phenological state during which drought occurs. On the whole lentil, groundnut and pigeon pea were found to experience lower drought induced yield reduction as compared to legumes such as cowpea and green gram. Usually yield reduction is greater when legumes experience drought during the period of the reproductive stage as compared to the vegetative stage. In the face of changing climate, our study provides useful information about the physiological base and research information for development of drought resistant legume species to improve alteration and flexibility of agricultural systems in the drought affected regions of the world.

Keywords: Drought, mitigation, pulses

Introduction

The world population continues to increase annually by more than 1%. Food production must obviously increase at the same annual rate to avoid a major nutritional crisis; thus, more food must be produced in an environment where there is severe competition for land and water, from industry and urban development (Postel, 2000) [53]. With the expected 40% increase in world population, the agricultural sector faces an immediate challenge to increase food production by 70% or even 100% by 2050 (Price, 2014; Bruinsma, 2009) [52, 51]. Such a compound increase in competition pushes agriculture to marginal areas, where water limiting conditions often constrain crop productivity. Besides the persistent water limitation and year by year fluctuations of meteorological circumstances in these marginal areas (e.g., semiarid environments) tend to be huge, and these variations significantly affect food security in these rain-fed systems. For example, groundnut yield in India wide-ranging between 550 and 1100 kg ha⁻¹ due mainly to rise and fall in annual rainfall (Reddy and Reddy, 1993) [54]. Not only quantity but also quality i.e. nutritional value of food, matters for the food security of such a great population. Apart from this challenge there is another task for agriculturist i.e. in a situation of adverse climate change which is having great impact on developing countries, we have to increase the productivity as well as nutritional quality of food grain.

All over the world major food requirement is fulfilled by three group of crops i.e. cereals, legumes and root/tuber crops. Legumes ranked second after cereal in terms of food production, which accounted for 27% of the world's primary crop production and contributed 33% of protein needs. They are grown in almost every climatic region and on a wide range of soil types. They also contributed more than 35% of the world's vegetable oil production, particularly from the processing of soybean and groundnut (Graham and Vance, 2003) [3]. These serve as key cash crop for more than 700 million smallholders in the developing countries, valued at about US\$ 31 billion annually. Most of that economic value comes from the export of soybean (83.8%), common bean (8.8%), groundnut (peanut) (4.9%) and chickpea (2.4%) (Abate *et al.*, 2012) [45]. Some legumes are grown as forages while others serve as important sources of soil nitrogen (N). These crops have positive impact on yield when grown in crop rotation or as cover crops with cereals. They have also been proved to increase soil carbon (C) and N content, improve the resistance of soil to erosion and lessen the incidence of certain soil pathogens (Sainju *et al.*, 2007; Bagayoko *et al.*, 2000) [46]. As manure in conservation agriculture, these miracle crops can enhance soil porosity and decrease bulk density (Sultani *et al.*, 2007) [48]. Promoting legume cultivation in developing countries could

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therefore emerge as an effective approach to achieving the goals of reducing poverty and hunger, improving health and maintaining environmental sustainability (Abate *et al.*, 2012)^[45]. World demand for legumes is expected to grow in the future, not only in developing countries, but also in the developed nations given the trend towards healthy and vegetarian dieting. As the remedial properties of legumes are better understood (Duranti, 2006)^[49] and the health hazard of consuming animal proteins is more widely recognized, also the demand for legume-based food products is expected to maintain its rising path. Everyday intake of legumes has been associated with reduction in the risk of cardiovascular diseases, diabetes, digestive tract diseases, and obesity (Duranti, 2006)^[49]. Consequently, global legume production increased from 150 million tons in the 1980's to 300 million tons in the 2000's. Legume production is dominated by soybean while pulses accounted for approximately 20% of total production during the same period (Gowda *et al.*, 2009)^[50]. The Food and Agricultural Organization (FAO) of the United Nations defines pulses as annual leguminous crops yielding from 1 to 12 grains or seeds of variable size, shape and colour within a pod.

Biologically, stress has also been defined as the overpowering pressure that affects the normal functions of individual life or the conditions in which plants are prevented from expressing their genetic potential for growth, development and reproduction. Agriculturally stress has been defined as phenomenon that limits crop productivity or destroys biomass. The continuous increase in atmospheric carbon dioxide (CO₂) concentration and the rise in mean ambient temperature are well known facts in the course of global change in climate (IPPC, 2012; Knutti *et al.*, 2016)^[29, 30]. In addition to that, climate change models forecast more frequent and further extreme events such as drought incidence or heat waves (Schär *et al.*, 2004; Fuhrer *et al.*, 2006; Mittal *et al.*, 2014; Fischer and Knutti, 2015; Teskey *et al.*, 2015)^[27, 31, 28, 35]. i.e. the abiotic stress. Abiotic stresses are those depend on the interaction between organism and physical & chemical environment. In case of soybean having yield potential of 7390kg/ha, it has been found that, it is giving yield of 1610kg/ha under stress (average yield loss by biotic stress is 666kg/ha and abiotic stress is 5120kg/ha) and abiotic stress is contributing 69.3% loss. Drought as well as elevated ambient temperature i.e. heat stress definitely cause extensive impacts on crop plants by upsetting critical physiological functions or stages including photosynthesis, mineral nutrient acquisition, transpiration, translocation via xylem and phloem, interactions between organs as well as yield quantity (i.e. nutritive value) and quality (Cottee *et al.*, 2014; Molina-Rueda and Kirby, 2015; Ramya *et al.*, 2015; Xu *et al.*, 2015)^[26, 32, 33, 36]. Drought is one of the most common environmental stresses that can affect growth and development of plants. Drought continues to be an important challenge to agricultural researchers and plant breeders. It is assumed that by the year 2025, around 1.8 billion people will face absolute water shortage and 65% of the world's population will live under drought environments. Tolerance to drought is a complicated parameter in which crops' performance can be influenced by several characteristics (Ingram & Bartels, 1996)^[62]. Droughts can negatively impact the yield of most cultivated crops, from monocotyledons C4 (i.e., maize) to eudicotyledons i.e. C3 cereals (such as wheat) and legumes (Olsen *et al.*, 2011; Pandey *et al.*, 1984; Peterson *et al.*, 1992)^[55, 56, 57]. Here our concern is with legumes. The yield of food legumes grown in

arid to semi-arid environments or dry-lands such as the Mediterranean (i.e., faba beans, chickpea and lentil), are usually variable or low due to terminal droughts that characterize these areas (Mafakheri *et al.*, 2010; Karou *et al.*, 2012)^[59, 4]. Even in non-dry-land countries like Brazil where precipitation is generally sufficient for legume (i.e., soybean) cultivation, water deficiency may still occur over a period of a few weeks, causing significant yield loss (Oya *et al.*, 2004)^[59]. Currently, the economically viable approaches to support crop production under drought are still limited (Li *et al.*, 2000)^[60].

In Indian situation here is an example. The production of cereals is projected to fall 41 percent, and pulses 11 percent, as agricultural growth in Maharashtra is set to decline 2.7 percent for the year 2015-16, after deficient rainfall in 278 of 355 talukas (sub-units of districts), according to the Economic Survey of Maharashtra 2015-16. The sparse rainfall has deterred sowing. During the 2015 *kharif* (April to October) season, 141.46 lakh hectare was sowed, 6% less than the previous year (150.97 lakh hectare). With rains failing in the *kharif* season, farmed area during the *Rabi* season is expected to decline 16 percent over the previous year. The production of cereals and pulses decreased 18.7 percent and 47 percent, respectively, in 2014-15. This year, 2015-16, the production of cereals is expected to decline 41 percent to 1.05 lakh metric tonne from 1.81 lakh metric tonne, while oilseeds are expected to grow nine percent.

More importantly, it is still unclear how the impact of drought on legume production varies with legume species, regions, agro-ecosystems, soil texture, and drought timing. Analyzing the results of field studies and drought manipulation experiments around the world, this study aims to better characterize the physiological factors that determine the extent of yield loss in legumes due to drought stress, which must be considered in agricultural planning to increase the resilience of legume production systems. The results of this study could also inform the development and selection of existing legume species, as well as better management for the drought affected regions of the world by testing whether these species become more or less sensitive to climate fluctuations, predominantly drought. For the purpose of this study, we define drought from the physiologic point of view where there is disturbance in normal physiological processes causing a reduction in grain yield due to water deficit. Our main objectives are:

1. To know how drought affects the physiological processes of legumes causing yield reduction and.
2. How to use this knowledge in minimizing legume yield reduction in drought affected regions.

Physiological Processes Affected By Drought Germination

The very initial as well as critical stage of plant life is the seed germination. The first effect of drought is, impaired germination and poor crop stand establishment (Harris *et al.*, 2002)^[14]. As we all are well known that water is the synonym to life. So obviously drought stress has been reported to severely reduce germination and seedling stand (Kaya *et al.*, 2006)^[15]. In a study on pea, drought stress impaired the germination and early seedling growth of five cultivars tested (Okcu *et al.*, 2005)^[20]. Moreover, in alfalfa (*Medicago sativa*), germination potential, hypocotyl length, and shoot and root fresh and dry weights were reduced by polyethylene glycol (PEG) induced water deficit, while the root length was

found to be increased (Zeid and Shedeed, 2006) ^[25]. The reason of this phenomenon is that germination cannot be possible without water, as enzyme activation cannot be possible devoid of water, which are responsible for the hydrolysis of reserved food product. Not only the simplification of food but also the translocation of monomer is not feasible in absence of water.

Morpho-physiological parameters

Moisture stress cause captivation i.e. breakage of water column within the plant means of which water is taken up from soil up to the tip of the plant, more so in large diameter vessels. Loss of water causes reduction in growth and wilting. This is also a reason of increased secretion of ethylene, causing abscission of leaf.

Leaf is the most important organ in plant body as it is the kitchen of plant providing food i.e. photosynthates to the whole plant body by the process of photosynthesis. The photosynthetically active leaf area highly influence individual plants and depends on the number and size of active (i.e. photosynthetic) leaves. Leaf emergence or appearance and expansion increase the active leaf area, while senescence decreases it (Lee *et al.*, 2012; Pantin *et al.*, 2012; Turner *et al.*, 2012; Blösch *et al.*, 2015; Esmailzade-Moridani *et al.*, 2015; Marquez-Garcia *et al.*, 2015) ^[80, 82, 83, 85, 90, 91]. The leaf area may be decreased under drought as compared to unstressed plants by a negatively influenced leaf expansion during leaf development or to some extent by shrinkage of previously expanded leaves as a consequence of water loss (Burling *et al.*, 2013; Scoffoni *et al.*, 2014) ^[87, 92]. While the minor or immature loss of leaf area caused by shrinkage is in general irreversible when mature leaves become again fully turgid after improving the water status of the plant by rainfall or re-watering, although the decreased area of mature leaves caused by negative effects on leaf expansion cannot be reversed after leaf expansion when secondary cell walls are synthesized. The reason behind this is that the drought or shortage of water reduce cell expansion as well as the cell division or mitosis. As a result not only the growth of leaf but also the whole plant stops. The first symptom of drought in plant is the reduction in emerging leaf area. There are examples in the literature demonstrating that when an organ is challenged by environmental stimuli, cell division and tissue expansion are affected to the same extent, suggesting that both processes are coupled. This was the case for pea leaves subjected to water deficits and tobacco leaves subjected to different levels of incident light (Granier, Turc & Tardieu 2000).

A smaller number of young leaves may be produced under drought or senescence may start earlier in older leaves. Actually when plants exposed to mild drought, there is production of abscisic acid (ABA) due to change in apoplastic pH, which is responsible for closure of stomata. Closing the door for CO₂ i.e. the main substrate for photosynthesis, plants undergo starvation. In this situation young leaves start feed on old leaves, i.e. remobilisation of nutrient starts. This process is carried out simultaneously with ethylene production which causes senescence of older leaf.

In case of severe drought, often senescence in such leaves is unusual and characterized by an in complete degradation of chlorophylls and proteins and by a poor nitrogen remobilization. Decrease in cell expansion and mitosis reduce the sink size and also sink activity, ultimately trim down the sink activity. Not only sink but also source is affected

similarly. Phloem transport and the nitrogen status of leaves are affected by drought, since the source/sink network is altered (Borrell *et al.*, 2001; Feller *et al.*, 2015) ^[86, 89]. Especially lowered sink strength in young leaves and reproductive organs contributes to these changes. Vegetative storage proteins may accumulate in senescing legume leaves under drought when nitrogen export capacity is limited (Lee *et al.*, 2014) ^[81]. Beyond a certain point, leaf senescence becomes irreversible and this leaf biomass is lost for the plant. Besides the onset and the velocity of leaf senescence, mechanisms involved in the catabolism of leaf constituents may be altered under abiotic stresses (Thoenen *et al.*, 2007; Feller *et al.*, 2008; Simova-Stoilova *et al.*, 2010) ^[93, 88, 84]. Young leaves may again be produced more rapidly during a recovery phase following the drought period (Blösch *et al.*, 2015) ^[85]. In this case the drought effects are not reversible on the level of already senesced leaves (irreversible loss of these leaves), but are partially reversible on the level of the whole plant (loss of mature leaves and production of new leaves). Newly emerging leaves may be positioned differently in previously stressed plants than in unstressed control plants. Often new leaves are produced from axillary buds in previously stressed dicotyledonous plants and not at the shoot apex as in control plants.

Low water stress greatly suppresses cell expansion and cell growth due to the low turgor pressure. Osmotic regulation can enable the maintenance of cell turgor for survival or to assist plant growth under severe drought conditions in pearl millet (Shao *et al.*, 2008). The reduction in plant height was associated with a decline in the cell enlargement and more leaf senescence in *Abelmoschus esculentus* under water stress (Bhatt & Srinivasa Rao, 2005) ^[63]. Development of optimal leaf area is important to photosynthesis and dry matter yield. Water deficit stress mostly reduced leaf growth and in turn the leaf areas in many species of plant like *Populus* (Wullschleger *et al.*, 2005) ^[77], soybean (Zhang *et al.*, 2004) ^[78] and many other species (Farooq *et al.*, 2009) ^[66]. Significant inter-specific differences between two sympatric *Populus* species were found in total number of leaves, total leaf area and total leaf biomass under drought stress (Wullschleger *et al.*, 2005) ^[77]. The leaf growth was more sensitive to water stress in wheat than in maize (Sacks *et al.*, 1997); *Vigna unguiculata* (Manivannan *et al.*, 2007a) ^[67] and sunflower (Manivannan *et al.*, 2007b & 2008) ^[68]. In soybean, the stem length was decreased under water deficit conditions (Specht *et al.*, 2001) ^[74]. The plant height was reduced up to 25% in water stressed citrus seedlings (Wu *et al.*, 2008). Stem length was significantly affected under water stress in potato (Heuer & Nadler, 1995), *Abelmoschus esculentus* (Sankar *et al.*, 2007 & 08); *Vigna unguiculata* (Manivannan *et al.*, 2007a) ^[67]; soybean (Zhang *et al.*, 2004) ^[78] and parsley (*Petroselinum crispum*) (Petropoulos *et al.*, 2008) ^[38]. Development of optimal leaf area is important to photosynthesis and dry matter yield. Water deficit stress mostly reduced leaf growth and in turn the leaf areas in many species of plant like *Populus* (Wullschleger *et al.*, 2005) ^[77], soybean (Zhang *et al.*, 2004) ^[78] and many other species (Farooq *et al.*, 2009) ^[66]. Reduced biomass was seen in water stressed soybean (Specht *et al.*, 2001) ^[74], *Poncirus trifoliata* seedlings (Wu *et al.*, 2008), common bean and green gram (Webber *et al.*, 2006) and *Petroselinum crispum* (Petropoulos *et al.*, 2008) ^[38]. Overall plant growth is disturbed by loss of water. If we compare between root and shoot, shoot or leaf growth is more sensitive than root growth.

Reproductive growth

Reproductive stage is very crucial for agricultural crops especially in cereal and legume crops, because flower induction, fertilisation, seed formation are the important stages which ultimately control the yield. Very few studies have been done to determine the effects of drought on the process of floral induction in cereals per se, which is difficult to separate from post-induction floral development in many cases (Saini & Westgate, 2000). Lalonde *et al.* (1997), suggested that the tapetal dysfunction leads to the loss of microspore orientation. The developmental anatomy of stress-affected anthers gives some hopeful hints about the metabolic proceedings that may be correlated to the malfunction of pollen development (Saini, 1997) [72]. Water shortage interrupts photosynthetic processes in vegetative plant tissues, particularly in leaves, consequential in a drop in the water soluble carbohydrate level in the anthers (Saini, 1997) [72]. Because of the disorders in the carbohydrate metabolism, the in time is unable to develop normally and insufficient amounts of reserve nutrients are stored in the pollen grains (Dorion *et al.*, 1996) [65]. Without starch to fuel pollen tube growth on the stigma, pollen tubes could not reach the ovule (Clément *et al.*, 1994) [64].

In legumes, drought that happened during vegetative periods is relatively more tolerable to plants even though they might experience retarded cell elongation, division and differentiation (Farooq *et al.*, 2009) [66]. Plants were still able to maintain their growth functions under stress because early drought might lead to immediate survival or acclimation where the plants modified their metabolic and structural capabilities mediated by altered gene expression (Chaves *et al.*, 2002).

Drought shows positive discrimination in the development of male rather than female inflorescence (Sangoi and Salvador, 1998) [101], which creates noteworthy fertilization failure. Normal starch build up during pollen development fails to occur in stress affected anthers (Sheoran and Saini, 1996) [102]. Within the legume group (i.e., soybean), drought-induced decrease in water potential and increase in ABA content (originated from root and/or leaf) in flowers were recorded, resulting in flower and pod abortion (Liu *et al.*, 2003) [100]. Here the impairment of carbohydrate and sugar metabolism due to drought during reproductive phase became the primary cellular level cause of yield reduction (Liu *et al.*, 2004) [79]. Drought during the reproductive phase in legumes (i.e., common bean) tends to reduce the total number of flowers per plant (by up to 50%) as well as the percentage of total pods located on the branches rather than on the main stem (Nuñez Barrios *et al.*, 2005) [107].

In pigeon pea, drought stress coinciding with the flowering stage reduced seed yield by 40-55% (Nam *et al.*, 2001) [18]. In chickpea same case was causing 45-69% yield loss as reported by Nayyar *et al.* (2006) [19]. Martínez *et al.* (2007) [16] reported that, drought during reproductive stage of common beans cause loss of about 58-87%. Samarah *et al.* (2006) [24] investigated that shortage of water at reproduction grounds 46-71% of yield in soybean. In case of cowpea this same reason is responsible for 60-71% of yield loss (Ogbonnaya *et al.*, 2003) [21].

Root parameters

A prolific root system can confer the advantage to support accelerated plant growth during the early crop growth stage and extract water from shallow soil layers that is otherwise

easily lost by evaporation in legumes (Johansen *et al.*, 1992) [37]. According to Postgate in 1998, certain plants, namely Fabaceae, form root nodules in order to associate and form a symbiotic relationship with nitrogen-fixing bacteria called rhizobia. Due to the high energy required to fix nitrogen from the atmosphere, the bacteria take carbon compounds from the plant to fuel the process. In return, the plant takes nitrogen compounds produced from ammonia by the bacteria.

The morphology and anatomy of roots largely determined through crop adaptability across different types of soil texture and their corresponding water availability (Purushothaman *et al.*, 2013) [104]. Xylem vessel size and number are among the most discriminating root traits in relation with their adaptability to different water regimes, at least within legume group with thinner vessel as an indicator of crop adaptability to soils with lower water availability (Purushothaman *et al.*, 2013) [104]. Chickpea, for example, is considered to be more adapted for fine textured soils than common bean, cowpea, or soybean as it has: (i) dense roots (even denser than pearl millet) and root thickening properties where the roots become thicker as soil moisture decreases, and (ii) a large number of thin vessels compared to other legume species which have broader vessels (Purushothaman *et al.*, 2013) [104]. As lateral movement of water in fine-textured soil is more restricted than those in coarser soils, these properties allow better absorption of soil water. These traits also allows chickpea to absorb water without requiring a wide gradient of water potential (Purushothaman *et al.*, 2013) [104]. Common bean, on the other hand, has broader vessels, indicating their suitability to soils with high water regimes and should be more productive under regular irrigation (Purushothaman *et al.*, 2013) [104]. Despite differences in root morphology and anatomy, chickpea as a species does not perform better than soybean or common bean in terms of yield. In contrast, soybean has lower yield reduction to drought as compared to common bean despite similarities in drought sensitivity or root characteristics (Purushothaman *et al.*, 2013) [104], indicating that improving yield performance could not be based on merely a single trait.

Root analysis requires destructive sampling, allowing only one-time measurement. Currently, recent development using root imaging techniques (i.e., minirhizotron tubes) allowed *in situ* root growth quantification over time, but this technique is expensive (Prasad *et al.*, 2008) [103]. So far, there has been limited breeding success based on root traits in legumes (Vadez *et al.*, 2008) [105]. Inexpensive root screening technique using deep-injected herbicide was used to measure the rate and depth of root development in cowpea and peanut (Prasad *et al.*, 2008) [103]. Using this method, crops were screened based on how fast and how deep their roots reached the herbicide and wilted. Crop roots that grew faster and deeper would wilt faster than those which did not. Developing crops that have deep rooting characteristic may become important as agriculture moves towards less water for irrigation (Wasson *et al.*, 2012) [106].

Selection for a deep and extensive root system has been advocated to increase productivity of food legumes under moisture-deficit conditions as it can optimize the capacity to acquire water (Subbarao *et al.*, 1995) [44].

The importance of root systems in acquiring water has long been recognized. The development of root system increases the water uptake and maintains requisite osmotic pressure through higher proline levels in *Phoenix dactylifera* (Djibril *et*

al., 2005). The root dry weight was decreased under mild and severe water stress in *Populus* species (Wullschleger *et al.*, 2005) [77]. An increase in root to shoot ratio under drought conditions was related to ABA content of roots and shoots (Sharp & LeNoble, 2002; Manivannan *et al.*, 2007b) [68].

Yield and yield attributive parameters

Yield and the associated parameters are highly dependent upon previous critical stages of plant life, such as germination, vegetative growth in particular with tillering or branching stage, flowering, seed filling stage etc.

Drought stress: In water stressed soybean the seed yield is far below when compared to well-watered control plants (Specht *et al.*, 2001) [74]. Water stress reduced the head diameter, 100-achene weight and yield per plant in sunflower. There was a negative correlation of head diameter with fresh root and shoot weight, while a positive one between dry shoot weight and achene yield per plant under water stress (Tahir & Mehid, 2001) [75]. Water stress for longer than 12 days at grain filling and flowering stage of sunflower (grown in sandy loam soil) was the most damaging in reducing the achene yield in sunflower (Reddy *et al.*, 2004) [71], seed yield in common bean and green gram (Webber *et al.*, 2006), and *Petroselinum crispum* (Petropoulos *et al.*, 2008) [38].

When compared to other crop groups, it has been found that the variation in yield reduction greatly depends on legume species, with some species (e.g., soybean, field pea, groundnut) exhibiting smaller variation in yield reduction compared to other species (e.g., lentil, pigeon pea, Bambara bean, common bean). Contrasting to our expectation that high variability in the response of root/tuber crops to drought might occur due to differences in plant families (e.g., Solanaceae, Euphorbiaceae, Convolvulaceae), our results indicated that most root/tuber species showed similar yield reduction under comparable water deficit. Across the three crop groups, we observed that there was a greater range (i.e., variability) of yield loss in legume (20-85%) and root/tuber groups (25-70%) compared to cereal (25-40%), except for anaerobic rice. As a group, the cereal crops also tended to exhibit lower yield reduction compared to either legume or root/tuber crops.

The yield of food legumes grown in arid to semi-arid environments or dry-lands such as the Mediterranean (e.g., faba beans, chickpea and lentil), was usually variable or low due to terminal droughts that characterize these areas (Karou and Oweis, 2012; Mafakheri *et al.*, 2010) [4, 59]. Even in non-dryland countries like Brazil where precipitation was generally sufficient for legume (i.e., soybean) cultivation, water deficiency might still occur over a period of a few weeks, causing significant yield loss (Oya *et al.*, 2004) [59].

Drought is the most damaging abiotic stress to soybean production, and in the USA, dry land soybeans yield approximately 60-70% less than irrigated systems (Egli, 2008). Drought stress in soybean reduced total seed yield and the branch seed yield.

Physio-biochemical processes

Shortage of water, produces changes in the ratio of chlorophyll 'a' and 'b' and carotenoids (Anjum *et al.*, 2003b; Farooq *et al.*, 2009) [62, 66]. A reduction in chlorophyll content was reported in drought stressed cotton (Massacci *et al.*, 2008) [70]. Water stress, among other changes, has the ability to reduce the tissue concentrations of chlorophylls and carotenoids (Kiani *et al.*, 2008), primarily with the production

of ROS in the thylakoids (Reddy *et al.*, 2004) [71]. The chlorophyll content decreases to a significant level at higher water deficits in sunflower plants (Kiani *et al.*, 2008) and in *Vaccinium myrtillus* (Tahkokorpi *et al.*, 2007) [76]. The foliar photosynthetic rate of higher plants is known to decrease as the relative water content and leaf water potential decreases (Lawlor & Cornic, 2002).

Leaf water potential is reported to control lots of biochemical processes. Some studies opined that determination of leaf water status in the morning and water content in leaves in the afternoon are potentially useful for screening drought tolerance in chickpea. Light interception and rate of photosynthesis can be also influenced via the spatial orientation of leaves including movement of turgid leaves (e.g. in legumes), leaf curling (e.g. in maize and other cereals) and wilting. (Save *et al.*, 1993; Werner *et al.*, 1999; Biskup *et al.*, 2007) [95, 94, 97]. Lower leaves in a dense stand may be exposed under drought to a higher photon flux density than the same leaves of non-stressed plants, since less photons are absorbed by leaves at the top of the plant. These changes are at least in early stress phases reversible. After re-watering (e.g. rainfall in fields), leaf rolling can be reversed within minutes to hours.

The first response of virtually all the plants to acute water deficit is the closure of their stomata to prevent transpiration water loss. Closure of stomata may result from direct evaporation of water from the guard cells with no metabolic involvement. This process of stomatal closure is referred to as hydro-passive closure. Stomatal closure may also be metabolically dependent and involve processes, which requires ions and metabolites, is known as hydroactive closure. This process seems to be ABA hormone regulated. The ABA is produced in roots and leaves during drought and transported to the guard cells. ABA causes the efflux of potassium ion, which ultimately responsible for the loss of turgor. The size of the stomatal opening is regulated by the turgor pressure and cell volume of the guard cells.

In general, photosynthetic capacity decreases before other cellular functions (e.g. respiration, intermediary metabolism associated with nutrient remobilization) (Hörtensteiner and Feller, 2002; Feller *et al.*, 2008) [98, 88]. The influence of previous water stress severity on the velocity and extent of photosynthesis recovery has been illustrated in kidney bean by Miyashita *et al.* (2005) [39] and Grzesiak *et al.* (2006) [40]. Decline in intercellular CO₂ levels results in the over reduction of components within the electron transport chain and the electrons get transferred to oxygen at pigment system I. This generates ROS including superoxide, hydrogen peroxide and hydroxyl radical. These ROS need to be scavenged by the plant as they may lead to photo-oxidation. Apart from this, the ROS cause damage to DNA, RNA, protein, lipid & chlorophyll, and thus damage membranes & change in cell metabolism. This disrupt the normal bilayer structure and results in membrane becoming exceptionally porous when desiccated, thus results in wilting and shrinkage. In extreme cases it results in impairment of the functioning of ions and transporters as well as membrane associated enzymes.

Water use efficiency

During early stages of moisture stress, transpiration is more affected or reduced than CO₂ per unit of water, and thus more photosynthesis and more photosynthesis and more formation of carbohydrate and thus more water use efficiency. But as

the stress continues, dehydration of the mesophyll tissue. Decrease in photosynthesis such that even higher external CO₂ concentration cannot do much and the water use efficiency decrease.

Osmotic Adjustment

As a mechanism, osmotic adjustment has been suggested as an important trait in postponing the dehydration stress in water scarce environments. Variation in osmotic adjustment among chickpea cultivars in response to soil drought has been observed, and seed yield of chickpea was correlated with the degree of osmotic adjustment when grown under a line-source irrigation system in the field. Contrarily, Serraj and Sinclair (2002) [41] found no yield advantage from osmotic adjustment in any crop. Nevertheless, further investigations are imperative to establish this controversy. As mentioned above, osmotic adjustment is accomplished with the accumulation of compatible solutes. Of these, proline is one amongst the most important cyto-solutes and its free accumulation is a widespread response of higher plants, algae, animals and bacteria to low water potential. Its synthesis in leaves at low water potential is caused by a amalgamation of increased biosynthesis and slow oxidation in mitochondria. Despite some controversy, many physiological roles have been assigned to free proline including stabilization of macromolecules, a sink for excess reductant and a store of carbon and nitrogen for use after relief of water deficit (Zhu, 2002) [43].

According to findings of Riccardi *et al.* (2001) [42] under drought stress, sensitive pea genotypes were more affected by a decline in relative water content than tolerant ones. In faba bean, determination of leaf water potential was useful for describing the drought effect, but was not suitable for discriminating tolerant from sensitive genotypes. This suggested that water potential was not the defining feature of the tolerance. Osmotic adjustment allows the cell to decrease osmotic potential and as a consequence, increases the gradient for water influx and maintenance of turgor. Improved tissue water status may be achieved through osmotic adjustment and/or changes in cell wall elasticity. This is essential for maintaining physiological activity for extended periods of drought.

Superoxide radical and its reduction product H₂O₂ are potentially toxic compounds, and can also combine by the Haber-Weiss reaction to form the highly toxic OH⁻ (Sairam *et al.*, 1998) [22]. Many reports show the deleterious effects of reactive oxygen species, whose production is stimulated under water stress (Blokina *et al.*, 2003) [13]. Reactive oxygen species cause lipid peroxidation, and consequently membrane injuries, protein degradation and enzyme inactivation (Sairam *et al.*, 2005) [23]. Oxidative stress may also cause protein oxidation, with a loss of enzyme activity and the formation of protease resistant cross-linked aggregates (Berlett and Stadtman, 1997) [12]. Oxidatively-damaged proteins accumulate in pea leaves subjected to moderate water stress (Moran *et al.*, 1994) [17].

Pulses/legumes

Chickpea (*Cicer arietinum* L.)

Morgan *et al.* (1991) [6], measured osmotic adjustment (OA) in six breeding lines grown in the growth chamber where stress was applied just before flowering. OA in the growth chamber was associated across these lines with increases in grain yield in field experiments conducted in 12 different field

sites over 2 years in Australia. The yield increases of high OA over low OA lines ranged from approximately null in low-water-deficit environments to approximately 20% in high-water-deficit environments. Leport *et al.* (1999) [7] tested six chickpea varieties in the field and measured their growth, photosynthesis, yield, water use and OA. While OA ranged across varieties from null to 1.3MPa, no relationship to rain-fed yield was found.

Moinuddin & Imas (2007) tested eight varieties under a line source irrigation system in the field where total seasonal rainfall was only 51mm. six cultivars were characterized by brown-red seed colour while two had pale yellow seed colour. OA was measured in leaves as well as specific osmolyte content, namely, sugars, proline, amino nitrogen and potassium. Potassium was the most important osmolyte at early growth stage stress, but with the increase in stress towards flowering, the contribution of the organic solutes to OA became more important. OA was associated with high RWC across varieties. Grain yield was positively and linearly correlated with high OA and RWC. The contribution of OA to chickpea yield was 26-60% with a relative advantage of the brown-red seeded varieties.

Turner *et al.* (2007) field tested for OA at the pod formation growth stage in progeny of high and low OA parents as determined earlier by Leport *et al.* (1999) [7] Yield was measured in eight F8 lines and parents in Western Australia (Mediterranean climate) and India (subtropical climate). OA varied among genotypes, but it was not consistent for genotypes over experiments and measurement methods. Yield was not associated with OA in any instance.

Pea (*Pisum sativum* L.)

Sánchez *et al.* (1998) [10] grew 49 genotypes subjected to drought stress in the growth chamber and measured OA, RWC and turgor. Nineteen of these genotypes were grown in the field under dryland and irrigated conditions in order to estimate yield. It was found that yield and HI under stress were positively associated across genotypes with the capacity for turgor maintenance under growth chamber conditions and that turgor was related to OA and to lesser extent to cell wall elasticity. The major solutes contributing to OA were sugars while the effect of accumulated proline was negligible in this respect.

Pigeon pea (*Cajanus cajan* (L.) Millsp.)

Subbarao *et al.* (2000) [9] tested 28 genotypes under a rainout shelter in the field where an irrigated treatment was compared with drought stress applied at several stages of reproductive development. OA was measured under stress in the field. Genotypes with the highest OA ranged from 0.28 to 0.48MPa. Grain yield was positively correlated with OA as measured at the early stages of the reproductive stage. It was negatively correlated with OA at the end of reproduction, probably because of the overriding effect of carbohydrate reserve remobilization into the grain.

Soybean (*Glycine max* (L.) Merr.)

A delayed wilting plant introduction was compared with a common cultivar ('Forrest') under stress and controls in the field over 2 years (Sloane *et al.* 1990) [8]. Data collected on plant water status, RWC and OP allowed to conclude that plant introduction had a better capacity for OA than Forrester and that the reduction in yield under drought stress was greater in the latter than the former.

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