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Defence Strategies of Annual Plants Against Drought

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1. Introduction

The irregular occurrence of drought periods accompanied by high temperature due to climatic changes influences the growth and yields of cultivars grown in agricultural fields. Many papers have reported the morphological and physiological response of plants to drought (Costa-Franca et al., 2000; Lin & Markhart, 1996; Lizana et al., 2006; Martinez et al., 2007; Sariyeva et al., 2009), but the effects of water supply on the physiological processes during different stages of crop development under field conditions have not been adequately studied. At field scale, drought and high (air/soil) temperature stress occur concurrently and not easily separable. Reduced evapotranspiration from a field due to drought is associated with increases in the temperature of the soil surface and that of the plant. In well watered plants, high temperature increases the water vapour pressure within the leaf and hence the rate of transpiration increases with the consequence of lower leaf water potential (Hsiao, 1994). Water stress may arise from either excess or deficit. Some days of waterlogging induce a rapid increase in the stomatal resistance which in turn reduces transpiration and net photosynthesis as a result of stomatal closure. These symptoms are similar to the responses to water deficit stress (Takele & McDavid, 1995). The flooding resulted in stomatal closure due to the leaf dehydration caused by increased resistance to water uptake as a result of the lowered permeability of roots (Amico et al., 2001). However, the more common water-related stress is the water deficit.

Plant responses to water stress differ significantly depending on (i) the intensity and duration of stress, on (ii) the plant species, and (iii) its stage of development. The most common field species can be categorized into three groups based on their sensitivity of drought. The tolerant group includes wheat, barley, sorghum, oat and alfalfa; the group with moderate sensitivity includes species as corn, sunflower, soybean, beans, peas; while potato, tomato and rice are belong to the extremely drought sensitive group (Heszky, 2007). The species ranged as tolerant are able to escape drought while those with moderate sensitivity can prevent the water deficit in their cells and tissues.

Various defence mechanisms have been developed in legumes in order to tolerate drought. The soil water content, high air/soil temperature and humidity adversely affect the shoot growth and yield of plants. Water deficit in the soil (-14.85 kPa) hampers the development and operation of root nodules of legumes. The high temperature (33°C) in the upper soil layer increases the number of nodules but decreases their size and the growth of the plants (Piha & Munns, 1987). Under severe dry conditions (-0.03- -0.5 MPa rooting medium water potential), the nitrogen-binding activity of root nodules decreases (Smith et al., 1988) resulting in the decrease of leaf area and leaf weight of the plants. Root characteristics, especially root length, root length density, and the number of thick roots, are important for plants to develop their aboveground parts by exploiting the soil available water. Expansive growth of leaves is also sensitive to water stress (Hsiao, 1994) and a short period (7 days) mild water stress (soil field capacity SFC 40%) already reduces the rate of leaf area development and leaf mass (Nemeskéri, 2001, Nemeskéri et al., 2010).

The changes in the morphology and anatomy of leaves as induced by drought are similar in many crops due to the same defence mechanisms (e.g. leaf movements). Most responses of plants to climatic factors such as water deficiency and high temperature under the field conditions are often different from that of plants grown in greenhouses (Nemeskéri et al., 2010). The cropping system (outdoor or greenhouse) can affect plant response to drought, this creates further complexity as concern the appraisal of on-set of stress. Therefore, it is important to examine plant traits variation in response to drought in order to create a sort of stress marker which can be used for the irrigation schedules and the modelling of crop transpiration. The determination of drought-stress markers is important in vegetables to maintain their yield production and food quality. In this chapter the defensive strategies of some annual crops (i.e. green bean and green pea) against drought and the relationship markers as measured in various developmental stages and yield level will be presented.

2. Defence strategies against drought

Plants have developed different defence strategies against drought during their evolution. The one possibility for them is to escape the drought when their most sensitive stage of development such as reproductive stage is completed before the drought. However, these crops with short ripening periods have generally low yields. Another one is the drought avoidance that is an ability of plants to maintain relatively high tissue water potential despite a shortage of soil-moisture. Two essential defence mechanisms operate in the plants to avoid the drought; one of them is the maintenance of water circulation in the plants that provide the deep root system and another one is to decrease the loss of water in the plants that can be achieved by restraining of transpiration and morphological changes. During long-term dry periods, the plants try to tolerate the water deficiency with low tissue water potential. The mechanisms of drought tolerance are maintenance of turgor through osmotic adjustment, increased cell elasticity and decreased cell size as well as desiccation tolerance by protoplasmic resistance.

2.1 Maintenance of the water status

The development of the root system is responsible for the water uptake and it contributes to the maintenance the water circulation inside plants. In summer days, the midday leaf water

potential usually decreases compare to early morning values due to higher rate of transpiration at noon. In the case of well-watered plants, the water deficiency in the leaves is promptly compensated. In the case of droughted plants, the dehydration of the roots increases their abscisic acid (ABA) synthesis which moves toward the leaves where accumulates leading to stomatal closure (Parry et al., 1992) and consequently the maintenance of water status. Under poor soil water content, the lives microorganisms in the soil are also retarded that causes low activity of mycorrhiza therefore, the nitrogen uptake through the root system decreases possibly causing a reduction of plant growth. In legumes plants, drought causes premature senescence of nodules and disturbance in the mechanisms of oxygen control that are essential for active nitrogen fixation hence the production of reactive oxygen species (ROS) may increase resulting in oxidative damage of nodules (Becana et al., 2000; Hernandez- Jiménez et al., 2002; Matamoros et al., 2003). Drought stress decreased a number of structural and functional traits (e.g. shoot dry weight, root dry weight, nodule dry weight, nitrogen fixation), however the nodular peroxidase (POX) and ascorbate peroxidase (APX) activities are increased significantly in nodules when droughted plants are in symbiosis with chickpea (Esfahani & Mostajeran, 2011). It was found that chickpea plants inoculated with various rhizobial strains the symbiosis showed difference tolerance level under drought condition. All rhizobial strains enhanced the tolerance of symbioses to drought stress, however the local strain contributed to higher increase in the antioxidant enzyme activities than the others (Esfahani & Mostajeran, 2011).

The proportion of root weight can also be changed as a consequence of drought; the root-to-shoot ratio increases under water-stress conditions (Nicholas, 1998). The proportion of soybeans roots was found to increase and that of the stem to decrease in the early reproductive development periods without irrigation. However, drought stress does not affect either the growth of roots or stem in the early stages of vegetative development (Hoogenboom et al., 1986). As opposed to soybean, there was a remarkable decrease in root and stem mass and pod weight of beans under water deficiency, respectively (Nemeskéri, 2001). The one strategy to overcome the limitation of leaf growth occurring under drought could be the rapid root growth, to allow the water uptake from deeper layers of the soil (Reid & Renquist, 1997). The growth rate of wheat and maize roots was found decreasing under moderate and high water deficit stress (Noctor & Foyer, 1998; Shao et al., 2008). It is another possibility is to decrease the endogen ethylene levels in the plants. It was found that accelerated ethylene levels could be responsible for growth inhibition, premature senescence and abscission induced by water deficits (Morgan et al., 1990). 1-aminocyclopropane-1-carboxylate (ACC)-deaminase enzyme impeding the ethylene production can be found in certain microorganisms. The plant growth promoting rhizobacteria containing this deaminase resulted in greater increase in root elongation and in root weight in the inoculated pea plants than uninoculated ones under drought stress conditions (Arshad et al., 2008).

2.2 Avoidance/reduction of the tissue water loss

During short-term drought intensive root elongation to the deeper part of the soil profile and the partial or total stomatal closure provide the avoidance of water loss for the plants. However, during longer dry periods the plants try to prevent the water deficit in the cells of vegetative and generative organs tissues by morphological and physiological changes. Even

mild water stress can reduce the rate of leaf area development leading to lower photosynthetic activity and low amount of produced biomass. Therefore the restricted growth of plants results smaller yield.

2.2.1 Stomatal functions

Transpiration provides continuous water and nutrients transportation. Stomata have important role in transpiration because they ensure the prevention of excessive water loss and also help control the leaf temperature. During the past decades, stomatal size and density have been used as an indicator of water loss (Singh & Sethi, 1995; Venora & Calcagno 1991; Wang & Clarke 1993a) but stomatal pore and width were rather considered to determine the capacity of stomata to reduce water loss (Aminian et al., 2011; Mohammady et al., 2005). However, the stomatal conductance showing the speed of water vapour evaporation depends on more plant-specific traits such as stomata density, leaf age and size, sub-stomatal CO₂ concentration, guard cell and cell turgor (Jones, 1992). The water use efficiency (WUE) as a key in determining productivity of a crop species is different in higher plants and relates to the stomata density under water limiting conditions. Higher stomatal frequency is associated with photosynthetic pathways and higher water use efficiency in C₄ compared with C₃ plants (Hardy et al., 1995).

The stomatal behaviour is directly influenced by signals received from the environment (e.g. light intensity) or mediated by roots (soil water deficit). Dehydrated root triggers the abscisic acid (ABA) synthesis which helps to the discharge potassium ions from bodyguard cells that causes stomatal closure and the retention of the water in the leaves (Gomes et al., 2004; Parry et al., 1992). This defence mechanism take place during short-term water deficiency (<7 days) when the dehydration of cells can be achieved by the restraining of transpiration. The long-term stomatal closure (10 days) results partial or total cessation of transpiration stream hence plants are not able to uptake water and nutrient from the soil. Consequently, the photosynthetic rate declines reducing the amount of photoassimilates for plant growth and reproduction. At high photosynthetically active radiation (PAR), drought combined with heat stress (40-45°C) result an increase in leaf temperature and temperature oscillations (±3-4°C), attributed to opening and closing of stomata (Reynolds-Henne et al., 2010). In general, highly variable leaf temperatures and stomatal opening within the relatively short intervals demonstrate a high stomatal sensitivity. However, the absolute stomatal responses are species-specific; for example bean stomata are more responsive to heat stress than clover (Reynolds-Henne et al., 2010). The rate of stomatal conductance with decreasing substrate water content decreased more in common bean genotypes than in cowpea ones. It means that beans (*Phaseolous vulgaris*) have a rapid and complete stomatal closure causing a decrease in the assimilation rate during drought while cowpeas (*Vigna unguiculata*) keep their stomata partially opened and have a lower decrease in their net photosynthetic rate under the same conditions (Cruz de Carvalho et al., 1998).

2.2.2 Changes in morphology

The maintenance of osmotic adjustment in the cells can be achieved by some attributes changed such as reduction of leaf size, leaf movement or leaf rolling under a short-term water deficiency. The trichome density (leaf hairs) not only provides a mechanical barrier to

insects but protects the plant from sunlight injury in the summer, decreases water loss by evaporation and enhances the transpiration-resistance (Du et al., 2009; Pfeiffer et al., 2003). Leaf movements are common defensive responses to drought stress in plants. Paraheliotropic leaf movement in response to stress occurs mainly in legumes and other species such as rice, maize, wheat and sorghum exhibit leaf rolling (Kadioglu et al., 2011; Matthews et al., 1990). Leaves move by means of turgor pressure changes at the pulvinus at the base of each lamina. In bean, paraheliotropism is an important property of the plants to avoid the photoinhibition. The extent of the leaf movements is increased as the water potential drops reducing light interception (Pastenes et al., 2005). Light and heat driving paraheliotropism can also occur in well-watered plants but it has a lesser extent than in water stressed plants. The other type of leaf movement is the leaf rolling operating as a dehydration avoidance mechanism reduces the effective leaf area therefore, the transpiration also reduces. The degree of leaf rolling in maize is linearly correlated with leaf water potential (Fernandez & Castrillo, 1999) while this is correlated with leaf osmotic potential and leaf temperature in rice (Ekanayake et al., 1993). Leaf rolling not only impedes the large water loss but protects the leaves of non-irrigated plants grown in the field from photodamage (Corlett et al., 1994).

The plant species living in arid habitat form epicuticular waxes on the outermost layer of the organs of plants to control the water flow across the cuticle and protect themselves from high radiation levels and prevent damage caused by UV light. It was found that water stress induced the accumulation of waxes on the leaf surface in peas and wax-rich varieties have significantly lower canopy temperature (Sánchez et al., 2001). A greater quantity of waxes also increases the reflection of the photosynthetically active radiation and UV-B light (Grant et al., 1995) which leads to the alleviation of heat stress.

2.2.3 Osmotic adjustment

Osmotic adjustment is an important physiological mechanism by which plants synthesize and accumulate compounds acting as osmolytes in cells in response to water deficits (Seki et al. 2007). When the decrease in water potential in plants is higher than 0.1 MPa then osmotic adjustment is generally occurs (Tari et al., 2003), causing the accumulation of sugars, amino acids, sugar alcohols and quaternary ammonium to lower the osmotic potential (Morgan, 1984; Gomes et al., 2010) to increase the osmotic pressure of the cells, drawing water into the cells and tissues hence contributing to the maintenance of turgor. Proline's role as an osmolyte or osmoprotectant in leaves of drought-stressed plants has been debated (Seki et al., 2007; Szabados & Savoure, 2009; Gomes et al. 2010). Indeed, proline has been demonstrated to confer drought stress tolerance to wheat plants by increasing the antioxidant system rather than increasing osmotic adjustment (Vendruscolo et al., 2007; Szabados & Savoure, 2009). However, other species (e.g. pea, castor bean) exposed to water deficit accumulate soluble sugars and proline contributing to the turgor maintenance by osmotic adjustment (Sánchez et al., 1998; Babita et al., 2010). Glycine betaine, which is one of the quaternary ammonium compounds, is considered to be the most effective osmoprotectant in many higher plants, because it protects the cells from environmental stresses by maintaining osmotic balance and stabilizing proteins, enzymes and membranes (Winzor et al., 1992; Yang et al., 1996; Gao et al., 2004). Many compounds were shown to have osmoregulator attributes; for example galactinol, raffinose have important roles in

improving stress tolerance in plants (Pennycooke et al., 2003; Nemeskéri et al., 2010), pinitol sugar alcohol accumulates in water-stressed legumes (Guo & Oosterhuis, 1995, 1997; Smith & Phillips, 1982) and in redbud trees (*Cercis canadensis*) to protect the plants from drought (Griffin et al., 2004). Under soil water stress of -0.6 MPa, maintenance of turgor in chick pea was due to a significant decrease in osmotic potential (osmotic adjustment) while in common bean it was due to maintenance of high leaf water potential but not to osmotic adjustment (Amede, 2003). Nevertheless, osmotic adjustment in broad bean in response to water deficit has not been found (Katerji et al., 2002; Khan et al., 2010).

Turgor maintenance can be achieved by osmotic adjustment and changes in the volumetric size of cells. The plants subjected to dehydration may avoid reduced water potential and maintain turgor by the reduction of their turgor-loss volume via shrinkage associated with elastic adjustment of their cell walls (Fan et al., 1994). Cell contraction means a reduction in cell size which is associated with plant resistance to water stress (Lecoeur et al., 1995). Cell size reduction has been reported in cassava plants (*Manihota esculenta*) grown under water stress (Alves & Setter, 2004). Citrus plants are able to develop elastic adjustment in response to water stress by the decrease in the volumetric modulus of elasticity (ϵ) (increase in cell wall elasticity) but do not develop osmotic adjustment as a drought tolerance mechanism under water stress conditions (Savé et al., 1995). Most of the bean varieties that presented high values of volumetric elastic modulus under well-watered conditions (above 3.7 ϵ) reduced significantly this parameter under water stress. Those bean cultivars decrease significantly their ϵ value and therefore increase their cell wall elasticity, while they present a positive drought resistance index and better resistance to the water stress (Martínez et al., 2007).

2.3 Drought tolerance

Drought tolerance is a complex property of the varieties including genetics, physiological or biochemical factors. Nevertheless the response of plant depends on the stage of development and strength and duration of the drought stress. For example, the water supply under flowering and seed development has important effect on the pods and seed yield and also on their quality in grain legumes. Under long-term drought periods (above 14 days), the growth of plants is retarded and they try to overcome the water deficiency by the decrease in water loss and leaf area or by increasing water use efficiency. During flowering, a longer period of water deficiency results in the loss of leaves and flowers that was much more intensive in large-leaved bean varieties than in those with smaller leaves (Nemeskéri et al., 2010).

When the avoidance of drought seemed to be insufficient by the changes of morphology and physiology, the plants undergo different biochemical and molecular genetic changes to maintain osmotic adjustment and the structure of cell membranes in order to avoid cell dehydration. Sugars act as osmotic compounds in protecting plants against drought and they contribute to the stabilization of cell membrane structures. A strong correlation between sugar accumulation and osmotic stress tolerance has been reported (El-Tajeb, 2006; Streeter et al., 2001). However, the accumulation and components of carbohydrates differ according to the individual responses of plant species. Decreases in sugars and oligosaccharides in *Arabidopsis* have been shown (Anderson & Kohorn, 2001) while in others, such as maize and rice, sugars accumulated during drought (Pelleschi et al., 1997;

Vue et al., 1998). Raffinose and sucrose content of leaves are increased by drought stress in the beans during flowering (Nemeskéri et al., 2010). Oxidative damage of the plant tissue is alleviated by a concerted action of both enzymatic and non-enzymatic antioxidant mechanisms. These antioxidant compounds react with free radicals and neutralize them, thus overcoming the damage caused by stress. Water deficit stress increases the lipid peroxidation in the leaves of young bean plants; however, the activity of catalase and superoxide-dismutase enzymes was high in the drought tolerant bean varieties (Zlatev et al., 2006). Numerous yet undetected water-soluble antioxidant compounds (ACW antioxidant capacity of water-soluble substances) may be responsible for the adaptation of plants to environmental stress factors. The ACW antioxidant contents in the leaves can be influenced by the stomata closure, because this is related to the ascorbic acid redox state of guard cells that control the stomatal movement (Chen & Gallie, 2004).

All responses to drought are controlled by complex mechanisms involved in the changes in gene expression. Micheletto et al., (2007) found that fewer genes ($n = 64$) were responsive in *Phaseolus vulgaris*, the more sensitive species, compared with *P. acutifolius* ($n = 488$) and only 25 genes were drought responsive in the roots of both species, at severe drought stress level of -2.5 MPa (midday) leaf water potential. Many genes (328) were induced in roots of *P. acutifolius* at severe drought compared with well-watered plants and 160 of them were repressed while in that of *P. vulgaris* the number of up-regulated gene was 49 and 15 genes were repressed. However, others (Meglič et al., 2008) revealed that nine genes were up-regulated in the leaves of drought stressed bean plants (*P. vulgaris*) in comparison with the well-watered plants and eight genes were repressed. The genes up-regulated belong to various previously reported functional categories characteristic for drought stress such as the late embryogenesis abundant proteins (LEA), synthesis of osmolytes, transcription factors, protein kinases, cellular- and carbohydrate metabolism while five of eight down-regulated genes belong to the functional category related to photosynthesis (Meglič et al., 2008).

2.4 Heat stress and tolerance

Under field conditions, high temperature stress ($30-35^{\circ}\text{C}$) is frequently associated with reduced water availability (Simoes-Araujo et al., 2003), thus the effects of drought and heat stresses on plant varieties is difficult to evaluate separately in the field. Anatomical changes under high ambient temperatures are generally similar to those under drought stress. At the whole plant level, there is a general tendency of reduced cell size, closure of stomata and reduced water loss, increased stomatal and trichomatous densities, and greater xylem vessels of both root and shoot (Añon et al., 2004). High temperature considerably affects anatomical structures not only at the tissue but also at cellular levels which result in poor plant growth and productivity (Wahid et al., 2007). This causes significant declines in shoot dry mass, relative growth rate and net assimilation rate in maize, pearl millet and sugarcane, though leaf expansion is minimally affected (Ashraf & Hafeez, 2004; Wahid, 2007). However, no doubt the reproductive phases such as gametogenesis and fertilization in various plants are the most sensitive to high temperature because a short period of heat stress can already cause significant increases in floral buds and opened flowers abortion (Foolad, 2005; Guilioni et al., 1997; Young et al., 2004).

The changes in the photosynthetic pigments indicate the thermo-tolerance of some species. An increased chlorophyll *a:b* ratio and a decreased chlorophyll carotenoids ratio

were observed in tolerant tomato genotypes under high temperatures (Camejo et al., 2005). At high temperature stress combined with soil water deficiency, chlorophyll *b* content in the leaves of French beans decreased during flowering, nevertheless the chlorophyll *a*:*b* ratio did not change in the genotypes in comparison with the control plants (Nemeskéri et al., 2010). However, common bean genotypes were detected to have significant differences in photochemical sensitivity to heat stress and also in the ability to modify their photochemical apparatus (Ribeiro et al., 2008). Plants are capable of adapting to different light environments by changing their photosynthetic pigment compositions. During continuous irradiation, the rapid transformation of chlorophyll *b* to chlorophyll *a* occurred in the leaves of light sensitive varieties and carotene ensures the great protection against photodamage (Procházková & Wilhelmová, 2004). One of the functions of carotenoids including β -carotene and xanthophylls is to act as an accessory pigment, capturing light and transferring energy to chlorophylls to drive photochemistry (Carvalho et al., 2011). However, carotenoids have another important function such as photoprotection of the reaction-centers, pigment-protein antennae, and cells and tissues (Li et al., 2009) and essentially as a non-enzymatic antioxidant (Arruda & Azevedo, 2009; Gratão et al., 2005). Other antioxidant compounds, enzymes and proteins also contribute to the defence of tissue against heat and light stresses. The activity of superoxide-dismutase (SOD) and ascorbate peroxidase enzymes was found to increase different extent with prolonged irradiation of the leaves and stimulated by high temperature, however, the activity of catalase enzyme was more sensitive to high temperature than to high irradiation (Ye et al., 2000).

A rapid heat stress results in the synthesis and accumulation of specific proteins designated as heat shock proteins (HSPs). Heat shock reduces the amount of photosynthetic pigments, soluble proteins, rubisco binding proteins (RBP) in darkness but increases them in light, indicating their roles as chaperones and HSPs (Kepova et al., 2005; Todorov et al., 2003). An increasing number of studies suggest that the protective effects of HSPs can be attributed to the network of the chaperone machinery, in which many chaperones (proteins) act in concert. The HSPs/chaperones also interact with other stress-response mechanisms such as production of osmolytes (Diamant et al., 2001) and antioxidants (Panchuk et al., 2002). The more HSPs activated in the distinct cellular compartments like cytosol, chloroplast, endoplasmic reticulum (ER), mitochondria and membranes the higher heat tolerance plants have. Five mitochondrial low molecular weight HSPs (from 19 to 28 kDa) were expressed in maize seedlings subjected to heat shocks (42°C), only one (20 kDa) was expressed in wheat and rye, suggesting the reason for higher heat tolerance in maize than in wheat and rye (Korotaeva et al., 2001). The stages of development of the plants in which heat shock genes cannot be induced are generally sensitive to heat stress but those involved by these genes expressed in high level are heat tolerance (Györgyey, 1999). In some cases, the heat shock genes do not provide advantages for the plants. The heat tolerant genes result in shorter internodes of main stem of the plants and reduce of biomass production in cowpea (*Vigna unguiculata* (L.) Walp.), on the other hand, after the first pod setting the ripening is accelerated and many pods are produced with few seeds as a result of these gene actions (Ismail & Hall, 1998).

The changes in anatomical structures at the tissue and cellular levels result in poor plant growth. There are great variations in heat sensitivity within and among plant species; for

example, in tomato, though plants are sensitive to high temperatures throughout the plant ontogeny, flowering and fruit set are the most sensitive stages; fruit set is severely affected by high day/night temperature above 35/26°C (Berry & Rafique-Uddin, 1988). A close significant correlation ($0,51 < r > 0,81$) was found between the high temperature and damage of the leaves in many of legumes such as soybean, pea, lupine and faba bean which expressed the extent of heat tolerance of these species. In legume plants, the mechanism of damage in cell membrane was the same independently of stress factors (Grzesiak et al., 1996). In general, heat stress singly or in combination with drought, is a common constraint during the anthesis and grain filling stages in pea and many cereal crops of temperate regions (Guilioni et al., 2003), and causes yield loss in common bean, *Phaseolus vulgaris* (Rainey & Griffiths, 2005) and groundnut, *Arachis hypogea* (Vara-Prasad et al., 1999).

3. Defence strategies in beans

In common beans, the mechanisms of drought tolerance principally include the development of an extensive root system (Micklas et al., 2006; Nemeskéri, 2001; Sponchiado et al., 1989) and efficient stomata closure (Barradas et al., 1994; Costa-Franca et al., 2000; Miyashita et al., 2005). It has been shown that the two high yielding *Phaseolus acutifolius* lines may rely on two different strategies. The first is characterized by a thin, deeply penetrating root with large mass and increasing stomatal conductance for one of the lines, while the other line developed a great mass of deeply penetrating roots and reduced the leaf expansion remarkably and stomata conductance (Mohamed et al., 2002). The bean variety that is more sensitive to drought has more intensive and earlier paraheliotropic leaf movement and the reduction in the water content of the leaves is faster under water deficiency than drought tolerant variety (Lizana et al., 2006). In spite of the fact that the many papers analysed the morphological and physiological response of beans to drought, the effects of water supply on the physiological processes during different stage of development of the plants have slightly studied under field conditions. Water use efficiency (WUE) is traditionally defined as the ratio of dry matter accumulation to water consumption over a season. Stomatal frequency positively correlates with the rate of water loss and stomatal conductance and associated with the water use efficiency (Hardy et al., 1995; Wang & Clarke, 1993b). Nevertheless these seemed to be cultivar-specific characteristics.

The pod numbers per plant are controlled mainly by genetic factors but the water use efficiency of the plant and stomatal function influenced the amounts of stock sized pods in French beans. Investigation of five French bean varieties grown in the field conditions revealed that the stomata density is higher on the abaxial surface of the leaves in the green-podded beans and lower on the adaxial surface than that of yellow-podded ones. Nevertheless, in both bean types, the stomata density was significantly larger on the adaxial surface of the leaves under mild water deficiency in comparison with irrigated plants in a dry year (Table 1). The analyse of WUE of green pod yield (WUE_y) shows that the green podded varieties use less water for one kilogram of yield than the yellow podded ones. Under water deficiency and serious terminal drought, increase in the stomatal resistance in the leaves of both bean types is related to the decrease in the pods weight. The transpiration is restrained as a result of the increase in stomatal resistance. That results the decline of CO₂ flow into the plants and the reduction of photosynthesis which leads to the decrease in yield.

Trait	Pod colour	Wet year			Dry year		
		I	WD	D	I	WD	D
Yield components							
yield (tons/ ha)	green	7.44 a	5.47 c	7.51 a	12.96 a*	11.13 a*	3.31 bc*
	yellow	7.36 ab	7.77a	8.18 a	7.00 b	4.73 bc*	1.46 c*
pod number/ plant	green	16.87 a	14.63 ab	14.11 ab	14.85 a	13.25 a	10.57 b*
	yellow	13.17 b	13.50 b	13.83 b	9.70 b*	9.92 b*	5.58 c*
total pod weight/ plant (g)	green	55.03 a	42.98 b	42.85 b	44.30 a*	35.15 ab	20.73 c*
	yellow	43.65 b	37.43 bc	31.20 c	35.19 ab*	30.98 b	13.02 c*
stock sized pods/ plant (g)	green	46.68 a	36.54 b	36.31 b	37.60 a*	28.12 b*	16.02 c*
	yellow	31.81 bc	30.10 bc	28.39 c	29.83 ab	25.08 b	9.32 c*
Water relations							
stomata number/mm ²							
abaxial surface	green	380.38 b	395.89 a	379.81 b	379.99 bc	412.56 ab*	402.54 b*
adaxial surface		23.98 f	34.68 f	26.68 f	69.26 c*	93.43 b*	109.14 a*
stomata number/mm ²							
abaxial surface	yellow	282.20 c	259.85 c	237.50 c	350.72 d*	370.46 cd*	429.90 a*
adaxial surface		55.63 e	65.58 d	73.52 d	73.98 c*	88.52 b*	85.15 b
stomatal resistance (s/cm)							
	green	1.638	1.781	1.759	1.079 d	1.289 cd	3.382 a*
	yellow	no data	no data	no data	1.497 c	1.527 c	3.098 b
SPAD value							
	green	33.36 a	33.53 a	33.42 a	36.27 c	38.70 b	42.95 a*
	yellow	34.54 a	35.86 a	38.60 a	33.73 d	35.61 c	38.65 b
WUEy (l/ kg/ m ²)							
	green	329.59 c	503.47 a	368.36 bc	206.14 d*	223.39 d*	624.03 b*
	yellow	286.37 bc	271.37 b	168.69 d	359.22 c*	441.17 c*	947.28 a*

I=irrigation, WD=water deficiency (I/2), D= dry, without irrigation, Data based on five varieties arranged in three replication in the field experiments.

Values in each row and coloumn having different letters are significantly different at the P<0.05 level using Duncan's multiple range test.

* Significant differences between years at the P<0.05 level

Table 1. Effect of water supply on yield components and water relation variables of green beans grown in the field conditions

Ramirez-Valejo & Kelly (1998) also found that stomatal conductance showed a positive association with yield, pod number, seed number and total biomass of common bean genotypes grown under water stress conditions. Reduction of the chlorophyll content in the leaves caused by water and heat stress and high irradiation contributes to the decrease in photosynthesis. The leaf of green bean varieties with yellow-green colour leaf is turned to dark green under prolonged severe drought in the field conditions as a result of the changes in the photosynthetic pigments. Eghball & Maranville, (1991) state that the effectiveness of utilising nitrogen and water are often associated. Chlorophyll itself also contains nitrogen; therefore, the measurement of chlorophyll content shows the utilisation of nitrogen and at the same time indicates the water utilisation. A close correlation ($r^2=0.9029$) was found between the SPAD values measured by a chlorophyll meter equipment and the chlorophyll content in the leaves so the SPAD values can be used for evaluation for the response of species to the drought and heat stresses in the field (Hawkins et al., 2009; Yadava 1986,). In additions, high positive correlations were proved between the chlorophyll content (SPAD) and the photochemical reaction indexes, and nitrogen demand (Perry & Davenport, 2007), and the measurement of drought stress in wheat (Ommen et al., 1999), the efficiency of transpiration in peanut (Krishnamurthy et al., 2007), the rate of photosynthesis, and the stomatal conductance in rice (Kato et al., 2004) during drought stress. During dry weather, the increment of chlorophyll content expressed by SPAD values indicates the nitrogen supply of the plant (Berzsenyi & Lap, 2003), and the changes in the glucose + fructose level in leaves (Nemeskéri et al., 2009). Under water deficiency, the trend in the increase of the stomatal resistance and SPAD values in the bean leaves is the same therefore, SPAD values can also be used as a water stress marker for the evaluation of drought tolerance of bean genotypes in field experiments.

In different stages of development, the plants respond in various ways to environmental stresses. It is known that bean yields are influenced by the climatic conditions during flowering. Before and during flowering, the stomatal resistance and chlorophyll content (SPAD) in the leaves significantly affect the yield. During the flowering period, a good correlation was found between the stomatal resistance and SPAD values ($r^2=0.587$) and pod weight per plants ($r^2=0.446$). According to these correlations, the chlorophyll content in leaves increased up 3.7 s/cm stomatal resistance values then it decreased. The pods weight of plants also decreased remarkably by the increasing stomatal resistance (above 3.7 s/cm). Another marker related to the pods weight per plants is the stomata number on the adaxial surface of leaves in bean. A higher number of stomata can be found on the abaxial surface than the adaxial surface of the bean leaves. However, that on the adaxial surface leaf seems to be more important in the restraining of transpiration. During flowering periods, the beans stomata number/mm² have significant influence on the stomatal resistance ($r^2=0.399$) and the lowest stomatal resistance (2.6-3 s/cm) can be measured by 85-105 stomata/mm² on the adaxial surface of the leaves. Larger stomata density on the adaxial surface of the leaves results in larger stomatal resistance producing the decrease in the pods weight of plants. During the pod ripening period, the stomata density on the adaxial surface of the leaves still have an influence on the yield of beans.

There are differences in the responses of the bean types to drought during the flowering period. Both the phytotron and field experiments illustrated that the yellow-podded green bean varieties respond to drought more sensitively than green-podded ones (Nemeskéri

et al., 2008, 2010). This was confirmed by the decrease in chlorophyll *a* and *b* components and the antioxidant capacity of water soluble (ACW) substances in the leaves of yellow-podded beans compared to the well-watered plants during flowering at severe drought stress in the phytotron, while there was not remarkable change in comparison with green-podded ones (Table 2). Under field conditions during the flowering period, the temperature (as minimum and maximum value) was similar to the treatment of 30/15 °C (day/night) in the phytotron that accompanied by water deficiency and often occurs in temperate zone. The average leaf weight and antioxidant capacity in the leaves were higher under field conditions than in the phytotron at 30/15 °C (day/night). However, the significant differences between the two bean types in photosynthetic pigment content and lipid soluble antioxidant (ACL) level in the leaves were also remained under field conditions (Table 2). The defence against drought had already begun prior to flowering when the correlation between the content of ACL in the leaves and seed yield ($r^2=0.607$) is so significant that it determined 61% of seed yield (Nemeskéri et al., 2010). Although the level of ACL antioxidants in the leaves decreased in nearly all genotypes during flowering, only those genotypes have high tolerance to drought accompanied with high temperature in which, the extent of the decrease is small or they are capable of re-increasing the production of ACL antioxidants during pod ripening (Fig. 1). These genotypes are able to produce seed yield above 1.0 tons /hectare under dry field conditions. The changes in the ACW antioxidants level in the leaves decreased similarly to ACL during flowering (Fig 2) but these antioxidants ensure primarily the protection against water deficiency (Chen & Gallie, 2004, Nemeskéri et al., 2010).

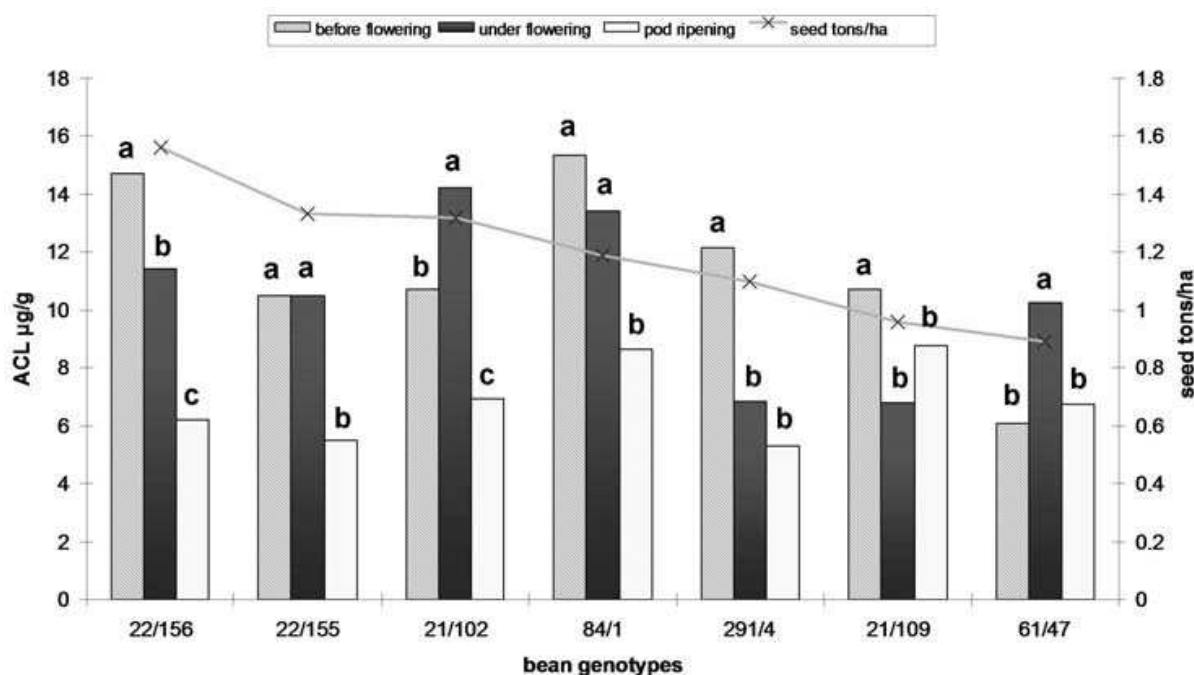
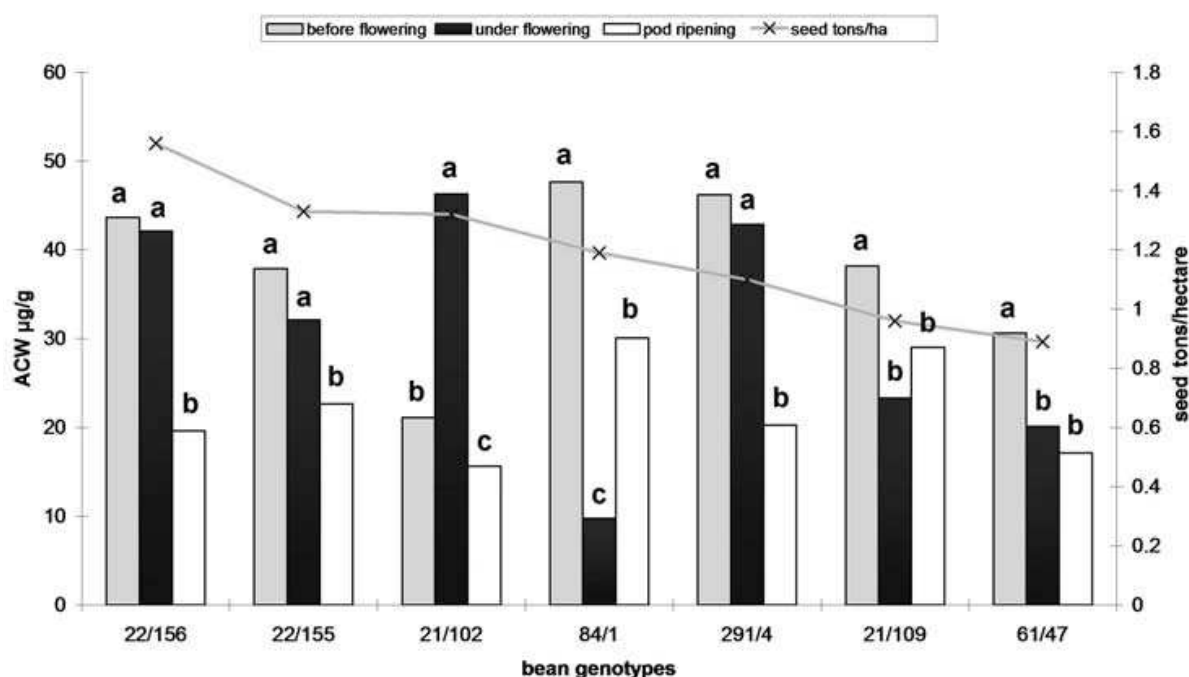


Fig. 1. Change in the level of lipid-soluble antioxidants (ACL) of bean leaves under dry field conditions.



Significant differences between phases of development are indicated by different letters at the P <0.05 level

Fig. 2. Change in the level of water-soluble antioxidants (ACW) of bean leaves under dry field conditions.

Bean groups	A			B				
	Yellow-podded beans			Green-podded beans				
Properties	25/15*	30/15	35/25	25/15	30/15	35/25	Yellow-podded beans	Green-podded beans
Average leaf weight (g)	0.34 b	0.19 c	0.12 d	0.41 a	0.18 c	0.20 c	0.64 a**	0.67 a**
Chlorophyll a (mg/g)	30.34 b	31.19 b	25.97 c	37.92 a	39.21 a	37.24 a	34.72 b	51.54 a**
Chlorophyll b (mg/g)	4.39 b	4.82 b	3.85 c	5.99 a	6.97 a	5.30 a	4.68 b	7.37 a
Carotene (mg/g)	25.15 c	35.63 b	22.33 c	31.30 b	41.77 a	29.27 bc	37.74 b	55.14 a**
Chlorophyll a/b	6.92 a	6.54 a	6.75 a	6.34 ab	5.74 b	7.14 a	7.44 a	7.01 a**
Chlorophyll/carotene	1.38 a	0.99 c	1.34 a	1.40 a	1.14 b	1.46 a	1.05 a	1.07 a
ACW (µg/mg)	17.07 a	9.81 b	8.11 b	3.51 d	4.70 c	2.64 e	18.23 a**	17.96 a**
ACL (µg/mg)	3.61 c	4.48 b	8.42 a	2.61 d	4.18 b	4.64 b	6.67 b**	8.05 a**

* 25/15 °C day/night with irrigation=control, 30/15 °C day/night combined with water deficiency=mild drought stress, 35/25 °C day/night= severe drought stress ** Significantly different from the mild drought stress (30/15 °C day/night) at the P <0.05 level

Table 2. Reactions of French beans with different pod types for drought stresses during flowering in the phytotron (A) and field (B) growing conditions

4. Defence strategies in peas

The pea of the food legumes has been less studied for drought tolerance than soybean and bean. Chickpeas (*Cicer arietinum* L.) and cowpea (*Vigna unguiculata* L. Walp.) cultivated almost completely arid and semi-arid zones of the world are continuously exposed to drought and high temperature during the flowering and maturity stages. Therefore these are well studied for drought tolerance. In cowpea, two types of drought tolerant mechanisms have been described at the seedlings age; one of them the drought tolerant pea lines stopped their growth after the onset of drought stress and turgidity was declined in all tissues of the plants for over two weeks while the other pea line was remained green for a longer time and the growth of the trifoliolate leaves continued slowly under drought stress (Agbicodo et al., 2009; Mai-Kodomi et al., 1999). The second reaction involved the combination of more defence mechanisms such as stomatal regulation (partial opening), osmotic control and material mobilization to the younger leaves (Agbicodo et al., 2009). Water stress induces the accumulation of soluble sugars in epicotyls of pea and the increase in free proline content contributing to osmotic adjustment, however, the degree of variation depends on the given cultivar (Sánchez et al., 2004). Genetic modifications of canopy structure of peas are expected to result in enhanced yield when water is a limiting factor. Genotype *af*, which has the leaflets transformed into tendrils, showed a faster CO₂ exchange rate, lower stomatal resistance, and lower canopy temperature under water stress than the genotypes with normal leaf (Alvino & Leone, 1993). Decrease in the soil water content resulted in the significant decrease of the leaf water potential and relative water content in the leaves in semi-leafless pea (*af*) variety that interrupted the vegetative growth and increased leaf senescence while the pea with normal leaf did not (Baigorri et al., 1999).

The green peas planted in spring utilize the soil moisture content well at the beginning of their growth. However, the next time the intermittent drought results in a decrease in the growth and yields. This may be the reason why few studies have been made to evaluate the factors influencing the water use and drought tolerance of green peas. Early maturing pea varieties exposed to intermittent water stress during the vegetative growth stage grow poorly and when this occurs during early stages of their reproductive phase, it results low yield. In wet years the chlorophyll content in the pea leaves and stomatal resistance are low but these are rising in dry years. The investigation of six green pea varieties grown in the field showed that excess of water supply results in larger increase in stomatal resistance in early ripening pea plants compared to the middle and late ripening ones, but the chlorophyll content in the leaves expressed in SPAD values is low in all groups (Table 3). Under dry weather conditions, the early and late ripening peas respond by high stomata density and stomatal resistance to the moderate water deficiency in comparison with well-watered ones, but the differences in WUE can be detected only in the late ripening group. Water deficiency significantly decreased the pod numbers and pod weights of the plant in the middle and late ripening groups. During both intermittent and prolonged drought periods the semi-leafless pea variety produced fewer pods and seeds with low weight in comparison with well-watered plants due to the high stomata density and stomatal resistance. While drought and heat resistance of chickpea genotypes have been evaluated by early flowering, plant vigor and pod setting under field conditions (Canci & Toker, 2009), these should be done by the stomata function and the changes in the chlorophyll content of the leaves used as a drought stress markers in green pea genotypes. Green peas are

Trait	Maturity	Wet year			Dry year		
		I	WD	D	I	WD	D
Yield components							
yield (tons/ha)	early	8.89 c	10.87 ab	12.38 ab	8.25 a	7.69 a*	6.13 bc*
	middle	10.61 b	12.07 ab	12.76 a	9.86 a	7.03 ab*	6.58 bc*
	late	12.04 ab	12.47 ab	11.35 ab	8.78 a*	6.67 bc*	4.61 c*
pod number/plant	early	3.75 b	3.80 b	3.80 b	3.19 c*	3.17 c*	2.83 c*
	middle	5.63 a	5.68 a	5.42 a	7.20 a*	5.98 b	5.44 b
	late	4.74 ab	5.39 a	4.89 ab	5.70 b*	3.80 c*	3.48 c*
average pod weight(g)	early	19.46ab	19.70 a	18.87 ab	15.29 b*	15.33 b*	12.80 c*
	middle	16.73 ab	15.13 ab	14.84 b	20.62 a*	14.78 bc	14.98 b
	late	16.34 ab	18.25 ab	15.29 ab	17.93 ab	12.30 c*	9.58 c*
seed number/plant	early	18.68 b	19.53 b	19.43 b	17.48 cd	18.40 cd	14.90 d*
	middle	26.86 a	23.62 ab	22.80 ab	40.08 a*	30.00 b*	29.20 b*
	late	22.63 ab	27.42 a	23.39 ab	33.85 b*	23.48 bc*	19.10 c*
100 green seeds weight (g)	early	43.68 a	41.30 a	42.71 a	43.54 a	44.57 a	44.77 a
	middle	25.03 cd	25.14 cd	24.39 d	20.96 d*	21.52 cd	23.52 c
	late	34.53 b	31.72 b	27.68 c	25.32 b*	29.53 b	27.58 b
Water relations							
stomata density (number/mm ²)	early	189.20 d	161.40 e	181.40 d	180.60 c	164.50 d	176.00 c
	middle	225.60 b	211.90 c	206.10 c	224.70 b	222.30 b	223.86 b
	late	226.90 b	229.00 b	240.30 a	218.08 b	243.70 a	236.48 a
stomatal resistance (s/cm)	early	1.613 a	1.540 ab	1.625 a	2.757 c*	3.538 ab*	2.653 c*
	middle	1.243 c	1.338 bc	1.316 bc	3.04 bc*	3.538 ab*	3.225 ab*
	late	1.163 c	1.174 c	1.188 c	2.885 bc*	3.538 a*	3.861 a*
SPAD value	early	39.45 c	41.50 b	42.86 a	45.42 c*	45.69 c	46.16 c
	middle	39.10 c	43.16 a	43.67 a	53.71 a*	53.25 a*	53.71 a*
	late	37.65 d	38.69 cd	40.52 b	50.52 b*	50.26 b*	50.24 b*
WUEy (l/ kg/ m ²)	early	231.27 a	189.14 a	166.07 b	66.25 cd*	65.58 cd*	75.69 c*
	middle	193.79 ab	172.69 ab	167.72 b	73.73 c*	90.33 bc*	99.67 b*
	late	218.97 a	206.77 a	233.17 a	89.92 bc*	103.85 ab*	137.98 a*

I= irrigation, WD=water deficiency, D=without irrigation, Values in each row and coloumn having different letters are significantly different at the P<0.05 level using Duncan's multiple range test. * Significant differences between years at the P<0.05 level

Table 3. Effect of water supply on yield components and water relation variables of green peas grown in the field conditions

generally grown for canning and freezing processing under irrigated conditions. However, the WUE of the varieties influences the yield quantity and quality, which is related to the drought stress markers in different stages of development. During flowering the chlorophyll content in the leaves (SPAD) and the stomata density can be related to the pods yield of the pea under dry weather conditions. This was confirmed by a close significant correlation found between SPAD and stomata density ($r^2=0.674$) and SPAD and pods weight ($r^2=0.375$) of green peas plants grown under non-irrigated conditions, respectively. The wax layer covering the adaxial surface of leaves contributes to the prevention of excessive water loss and because no stomata can be found here, the transpiration goes through the stomata on the abaxial surface of leaves. Under dry conditions (SFC 40%), during pod ripening the stomatal function seems to have a greater influence on the pods weight of the pea than during flowering period. This time the pod yields of the plants decreased significantly when the stomata resistance based on the high significant correlation between the stomata resistance and pods weight ($r^2=0.557$) was rising above 4 s/cm. The stomatal function influences the water supply of the green pods in the late ripening cultivars during flowering periods, however the chlorophyll content in the leaves affects the green seed weight which is confirmed by a close correlation between stomata resistance and pod weight ($r^2=0.994$) and SPAD and seed weight ($r^2=0.634$), respectively. During the pod ripening period, above 4 s/cm stomata resistance, the pod weight and seed weight of plants decreased significantly in the middle ripening group but the decrease was very intensive in late ripening ones under dry field conditions. During the pod ripening period the late ripening green pea varieties are much more sensitive to drought than the middle ripening ones that was confirmed by the relationship between the drought stress markers and yield.

5. Drought stress markers and yield

Breeding for drought tolerant varieties has been accomplished by selection for seed yield under field conditions but such procedure requires full season field data and this is not always an efficient approach. The changes in morphology including the decrease in growth and leaf size, leaf movements etc. are less appropriated to measure the water status of plants. These can be used with low efficiency for evaluation the drought adaptation and irrigation scheduling. The changes in physiological attributes of the plants rather indicate the disturbance of water supply and these can be used to determine the degree of drought tolerance of the varieties even though the reproducible experimental environments can be hardly achieved in the field. The identification of stress markers is difficult because they can vary on the crop species and in many cases the factors operating in the defense of damage caused by environmental stresses are or are not activated under different periods of development. The legumes of the field crops with moderate sensitivity to drought have the most various defence strategies. The deeply penetrating roots with large mass and large density in trichomes on the leaves in soybeans ensure the maintenance of the sub-optimal water status of the plants (Du et al., 2009; Nemeskéri, 2001) also after the onset of a moderate water deficit. However, the root characteristics cannot be considered as drought stress markers because their measurement is rather difficult. The stomata density on the adaxial surface on leaves and the high trichomes density on the leaves decreases the water loss in green beans. Although the stomata cannot be found on the adaxial surface on the leaves in green peas, the wax layer contributes to the defense against high temperature and water deficiency.

The responses of plants to stresses depended on many factors such as the phenological stage and time and strength of stresses. Under mild drought, the higher stomata density on the abaxial surface of the leaves in green beans can already be detected during flowering but in the green pea this occurs only during green pod ripening (Table 4). In terminal drought stomatal action expressed as stomata resistance is intensive in all stages of development in beans but it is very intensive in green peas only during green pod ripening. The water supply, during flowering period, is considered to determine the yield in the legumes. However, the crop species use different defence strategies against drought occurred this time. For example, during flowering the stomatal resistance and the stomata density on the adaxial-side of leaves are related to the quantity of pod yields in bean but at the same time the chlorophyll content in leaves (SPAD) in green peas has a great effect on the pods yield while the stomata resistance has not. The changes in the photosynthetic pigment seemed to be determinative to the green pod yields in both species during pod ripening and these can be used as drought stress markers for the selection of genotypes with drought tolerance. During flowering the defence of plants against damage from climatic stresses occurs in many stages in bean varieties. At first, the carotene and raffinose contents of leaves increase, then with rises in temperature additional protective mechanisms are activated e.g. the production of raffinose, glucose and sucrose are increased and the level of ACL antioxidants in the leaves rises (Nemeskéri et al., 2010). During the seed development in the pods the defence is going on by the increase in the level of antioxidants against severe drought and high temperature. The tolerance to water deficiency is related to the content of ACW antioxidants in the leaves and the tolerance to high temperature by the ACL antioxidants ensures the high seed yields so the changes in the antioxidants levels can be used as stress markers in the breeding for drought resistance.

Species	Treatment	Stomata number/mm ² abaxial side			Stomata number/mm ² adaxial-side			Stomatal resistance s/cm		
		BF	F	PR	BF	F	PR	BF	F	PR
Green bean	Irrigation	359.58 cd	424.89 b	311.12 e	72.92 c	84.96 b	56.73 d	1.74 cd	1.34 de	1.43 d
	Water deficit	369.40 c	458.31 a	346.86 d	87.66 b	112.80 a	72.63 c	1.79 c	1.40 d	1.18 e
	Dry	410.05 b	455.71 a	382.89 c	105.96 a	103.55 a	81.97 bc	4.11 a	3.39 b	3.40 b
Green pea	Irrigation	205.94 b	165.70 d	262.68 a	-	-	-	1.90 d	0.90 e	4.02 c
	Water deficit	199.58 b	181.57 c	263.74 a	-	-	-	2.43 d	1.41 de	4.59 bc
	Dry	205.07 b	183.11 c	259.98 a	-	-	-	1.92 d	1.29 de	5.21 b

BF= before flowering, F=under flowering, PR=pod ripening

Table 4. Stomata density and stomatal resistance in comparison with green pea and green beans

6. Conclusion

The negative impact of climatic stresses on agricultural productivity can be reduced by a combination of genetic improvement. Genetic improvement of crops for stress tolerance is relatively a new endeavour that would be successful if the relationship between the stress markers and yield were revealed. The plants adapt their morphology and physiology processes to limit damage(s) caused by environmental stresses, however, this requires high energy (depending on the stress level) and leads to the decrease in yield. Crop plants generally use more than one defence mechanism at a time to cope with drought. Defence has physiology and molecular basis depending on stage of development. The defence strategies of field crops with moderate sensitivity to drought have been presented especially in green beans and green pea populations. These species have different light and heat demands and use different defence strategies in their stages of development under field conditions. During flowering periods, the changes in the photosynthetic pigments, stomatal density, stomatal resistance and antioxidants levels can be considered to the drought stress indicators in the case of green bean. At the same time, the chlorophyll contents in leaves and stomatal resistance are related to the yield so these can be regarded as drought stress indicators in green peas. The correlations between the drought stress marker attributes and yields can be used for screening large number of genotypes and selecting them for drought tolerance under field conditions. These stress markers measured in the field indicate the disturbance of water supply in the crops and can also be used either for the irrigation schedules in crop production or the development of a transpiration crop model. These can also be used for the selection of genotypes with drought tolerance in the course of breeding.

7. References

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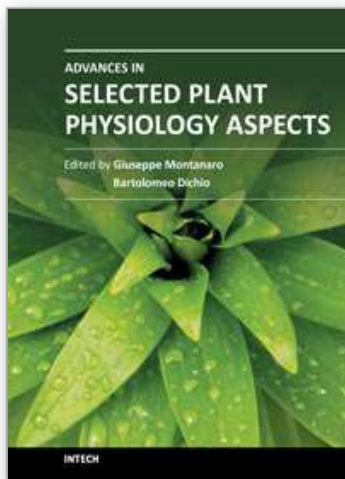
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