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Abiotic Stress Responses in Legumes: Strategies Used to Cope with Environmental Challenges

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Legumes are well recognized for their nutritional and health benefits as well as for their impact in the sustainability of agricultural systems. The threatening scenario imposed by climate change highlights the need for concerted research approaches in order to develop crops that are able to cope with environmental stresses, while increasing yield and quality. During the last decade, some physiological components and molecular players underlying abiotic stress responses of a broad range of legume species have been elucidated. Plant physiology approaches provided general outlines of plant responses, identifying stress tolerance-related traits or elite cultivars. A thorough identification of candidate genes and quantitative trait loci (QTLs) associated with these traits followed. Model legumes like *Medicago truncatula*, *Lotus japonicus*, and more recently, *Glycine max* provided valuable translational approaches for dissecting legume responses to abiotic stresses. The challenge now focuses on the translation of the information gained in model systems in controlled environments to crops grown under field conditions. In this review, we provide a general overview of the recent achievements on the study of abiotic stress responses in a broad range of model, grain and forage legumes species, highlighting the different approaches used. Major accomplishments, as well as limitations or drawbacks are discussed across the different sections. Some perspectives regarding new approaches for screening, breeding or engineering legumes with desirable abiotic stress resistance traits are anticipated. These advances will support the development of legumes better adapted to environmental constraints, tackling current demands on modern agriculture and food production presently exacerbated by global climate changes.

Keywords abiotic stress, genomics, model and crop legumes, molecular breeding, phenotyping, physiology, quantitative genetics

I. INTRODUCTION

Legumes (*Leguminosae* or *Fabaceae*) belong to the second most important plant family in agriculture after the *Poaceae* or grass family. They provide the largest single source of vegetable protein in human diets and livestock feed (forages), and contribute to agriculture, the environment and human health (reviewed in Graham and Vance, 2003; Young *et al.*, 2003; Dita *et al.*, 2006). In developing countries, grain legumes or pulse crops represent an important component of local food consumed and are a key source of protein in the diets. They provide an input-saving and resource-conserving alternative because they fix atmospheric nitrogen, thus reducing the need for chemical fertilizers while enhancing overall crop productivity. In farming systems, legumes are often used as an inter-crop (e.g., combined with cereals) or in crop rotation resulting in a decrease in pests, diseases and weed populations, while enhancing the overall farm productivity and income of smallholder farmers. Based on these attributes, it is tempting to claim that legumes are one of the most promising components of the Climate Smart Agriculture concept (FAO, 2013).

Abiotic stresses play a major role in determining crop and forage productivity (Boyer, 1992; Rao, 2013), and also affects the differential distribution of the plant species across different types of environments (Chaves *et al.*, 2003). Climate change exacerbates abiotic stress on a global scale, with increased irregularity and unpredictability, and as a result, adaptation strategies need to be developed to target crops to specific environments (Beebe *et al.*, 2011). Within a single production region, a crop may encounter both excess and deficient moisture, depending upon the year, or even within the same growing season, when rainfall distribution becomes erratic. Higher temperatures will probably accelerate mineralization of soil organic matter, making soil constraints more intense (Lynch and St. Clair, 2004), and these in turn can limit root penetration and plant development, further intensifying the effects of unfavorable climate (Beebe *et al.*, 2013a). Furthermore, interactions between different stress factors will likely increase damage to crop yields (Beebe, 2012; Yang *et al.*, 2013).

A remarkable feature of plant adaptation to abiotic stresses is the activation of multiple responses involving complex gene interactions and "cross-talk," with many pathways at the whole-plant, physiological, biochemical, cellular and molecular levels (Grover *et al.*, 2001; Le *et al.*, 2006; Atkinson *et al.*, 2012). Knowledge about how these biological processes are modulated by the abiotic stresses is still a challenge pursued by both public research efforts and the private sector.

Like many other crops, legume production is affected by unfavorable environmental conditions. During the last decade, researchers have focused on elucidating the various physiologic and molecular components underlying abiotic stress responses of a broad range of species, both model and crops. Although plant physiology provided a general overview of plant responses, identifying stress tolerance-related traits or the generation of better performing cultivars through breeding, further elucidation of the genetic basis of these important traits (as major responsible genes or associated Quantitative Trait Loci, QTLs), integrating molecular biology and genomics approaches, is needed to further dissect, and eventually profit from, the mechanisms underlying plant adaptation to abiotic stresses (Mir *et al.*, 2012). Equally important will be to advance the understanding of the plant responses to the combination of multiple abiotic stresses (Mittler and Blumwald, 2010; Yang *et al.*, 2013), especially on crop species who commonly face these challenges under field production.

This review focuses on the recent achievements in the study of legume responses to abiotic stresses, highlighting the different molecular and physiological approaches used to improve our understanding of the biology of the complex responses (Table 1). In addition, some perspectives regarding new approaches to breed or engineer plants with desirable traits are provided, aiming to develop legumes better adapted to environmental factors limiting agricultural productivity.

II. ABIOTIC STRESS RESPONSES IN MODEL LEGUMES

The study of the unique biological mechanisms used by legumes in response to stress conditions has been facilitated by the establishment of several model species. *Medicago truncatula* and *Lotus japonicus* have been the primary models developed to investigate plant-microbe interaction and nitrogen fixation. As sequencing costs have declined, additional legume genomes have been sequenced, and the funding available to crops such as *Glycine max* has enabled these to be developed to the status of genetic models in their own right (Cannon, 2013). Being the most important legume crop, the use of *G. max* as a model species presents several advantages over the *M. truncatula* or *L. japonicus*, providing valuable outputs in questions related to yield or grain production (e.g., grain filling or pod abortion), susceptible to be transferred among others cultivated legume. The release of almost complete genome sequences for these species (Young and Bharti, 2012) combined with the existence of genetic transformation protocols (Stewart, 1996; Aoki *et al.*, 2002; Araújo *et al.*, 2004) make them important tools to dissect the molecular mechanisms underlying legume adaptation to abiotic stresses. Several mutant populations and resources have been developed constituting essential tools for reverse genetics approaches aiming to understand gene function (Tadege *et al.*, 2009). Additionally, the development of several bioinformatic tools, such as the LegumeIP (Li *et al.*, 2012) and the Legume Information System (LIS) (Gonzales *et al.*, 2005) enables comprehensive queries based on gene annotation, gene family, synteny and relative gene expression. Bottom line, model legumes are now exciting platforms to functionally validate and derive new strategies to obtain improved legume phenotypes.

A. Drought Stress

Photosynthesis, together with cell growth, is among the primary processes to be affected by drought (Chaves, 1991). Another impact of water deficit on carbon metabolism results in changes in the pool of sugars used for signaling cellular processes or substrates for biopolymers like cellulose, starch and proteins (Chaves *et al.*, 2009; Liu *et al.*, 2013). Thus, it is tempting to claim that under drought the yield and quality of the harvested plant parts (e.g., grains, biomass, and stalks) may rely on the cross-talk of regulating processes at the whole plant level. Given its historical role in Australian agriculture, *M. truncatula* became a valuable resource for functional plant biology, namely on understanding how a plant interacts with its environment (Rose, 2008). Nunes *et al.* (2008) evaluated the two main components of drought resistance, drought avoidance and drought tolerance mechanisms in the mature *M. truncatula* cv. Jemalong. In this study and under mild stress conditions, when the soil water content decreased to one-half of its maximum, *M. truncatula* plants maintained identical leaf relative water content (leaf RWC), net CO_2 fixation rate, photochemical and

TABLE 1
Some of the major achievements in breeding for resistance to abiotic stress in legume crops with indication of potential inputs from knowledge on model legumes

Species	Breeding Achievement	Traits Addressed	Potential Input from Model Legumes
Drought			
Alfalfa	Selection of **drought tolerant** wild and cultivated germplasm (Ray *et al.*, 1998, 2004; Condon *et al.*, 2004; Zhang *et al.*, 2005; Han *et al.*, 2007, 2008; Kang *et al.*, 2011)	• Higher WUE • Vigorous root growth • Higher osmolytes and antioxidants accumulation • Higher biomass partitioning into the harvested product • Cuticular wax accumulation	**1) From *M. truncatula*:** QTLs identification related to seed vigor (Vandecasteele *et al.*, 2011) QTLs related to drought resistance *in vitro* and under greenhouse conditions (Badri *et al.*, 2011) miRNA identification involved in drought stress (Szittya *et al.*, 2008; Wang *et al.*, 2011) **2) From *G. max*:** QTLs identification for multiple traits suggested that several had pleiotropic or location-linked associations (Charlson *et al.*, 2009) QTLs identified for improved drought resistance and seed yield (Du *et al.*, 2009) miRNA identification involved in drought stress (Li *et al.*, 2011) **3) From *L. japonicus*:** miRNA identification involved in drought stress (Hu *et al.*, 2013)
Chickpea	Selection of **drought escaping** germplasm (Summerfield *et al.*, 1990; Kumar & van Rheenen, 2000; Berger *et al.*, 2011)	• Early maturing • Deeper profuse root system • Increased yield under terminal drought	
	Selection of **drought avoidant** germplasm (Saxena, 1984; Chandra *et al.*, 2004a; Gaur *et al.*, 2008; Vadez *et al.*, 2012a)	• Low leaf conductance • Smaller leaf canopy • Soil water extraction	
	Selection of **drought tolerant** germplasm (Krishnamurthy *et al.*, 2010; Zaman-Allah *et al.*, 2011a,b)		
Common bean	Selection of **drought escaping** germplasm (White & Singh, 1991)	• Early maturing • Deep rooting • Stomatal control	
	Selection of **drought avoidant** germplasm (Asfaw & Balir, 2012, Beebe *et al.*, 2013b, c; Devi *et al.*, 2013)	• High grain yield • High photosynthate remobilization	
	Selection of **drought tolerant** germplasm (Beebe, 2012; Beebe *et al.*, 2008, 2013a, b; Rao *et al.*, 2009, 2013; Rao 2014)		
Cowpea	Selection of end-of-season **drought escaping** germplasm (Edlers & Hall, 1997)	• Early maturing • Growth hampering • Stomata control	
	Selection of **drought avoidant and tolerant** germplasm (Ismail *et al.*, 2000; Hall *et al.*, 2004; Muchero *et al.*, 2009, 2010)	• Stem greenness • Delayed leaf senescence • Osmotic adjustment	
Faba bean	Selection of **drought escaping** and **drought tolerant** germplasm (Nerkar *et al.*, 1981; Amede *et al.*, 1999; Link *et al.*, 1999; Khan *et al.*, 2007; Patrick & Stoddard, 2010; Khazaei *et al.*, 2011, 2013a,b)	• Early maturing • Terminal inflorescence types • Low plant height • Increased WUE • Reduced leaf temperature • Increased water content	

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TABLE 1
Some of the major achievements in breeding for resistance to abiotic stress in legume crops with indication of potential inputs from knowledge on model legumes *(Continued)*

Species	Breeding Achievement	Traits Addressed	Potential Input from Model Legumes
Lentil	Selection of **drought escaping** germplasm (Erskine *et al.*, 2011) Selection of **drought tolerant** cultivated and wild germplasm (Stoddard *et al.*, 2006)	• Early maturing, • Early growth vigor • Rapid root growth • lower cell membrane injury • High seedling growth • Osmotic regulation • High WUE	
Pea	Selection of **drought resistant** and **tolerant** germplasm (Grzesiak *et al.*, 1997; Sanchez *et al.*, 1998, 2001; Hernandez *et al.*, 2000; Alexieva *et al.*, 2001; Hernandez & Almansa, 2002; Gonzalez *et al.*, 2002; Benjamin & Nielsen, 2006; Charlton *et al.*, 2008)	• Smaller root/shoot ratio • Increased epicuticular waxes • Deeper roots • Increased content of antioxidants • Increased osmolarity • Turgor maintenance	
Pigeon pea	Selection of **drought tolerant** cultivated germplasm (Odeny, 2007)	• Deep root • Osmotic adjustment • Photosynthetic maintenance • Polycarpic flowering habit	
Water logging			
Lentil	Selection of **water logging resistant** germplasm (Stoddard *et al.*, 2006)	• Large aerenchyma or air-spaces in roots • High stomatal conductance	
Salinity			
Alfalfa	Selection of **salinity avoidance** cultivated germplasm (Vaughan *et al.*, 2002) Selection of **salinity tolerant** cultivated germplasm (Scasta *et al.*, 2012)	• High fibrous roots	**1) From *M. truncatula*:** QTLs associated with the response of leaves, stem and roots to Na+ and K+ uptake were mapped to several genomic regions (Arraouadi *et al.*, 2012) Identification of salt adapted genotypes (Mhadhbi *et al.,* 2011; Elmaghabri *et al.*, 2013) Identification of transcription factors associated with improved salt tolerance (De Lorenzo *et al.*, 2007; Gruber *et al.*, 2009; Zahaf *et al.*, 2012) **2) From *G. max*:** Identification of salt adapted genotypes (Shao *et al.,* 1986; An *et al.,* 2002; Luo *et al.*, 2005; Phang *et al.,* 2008; Ma *et al.*, 2010) Major salt tolerance QTLs conserved between wild and cultivated species (Lee *et al.*, 2004; Hamwieh & Xu, 2008)
Chickpea	Selection of **tolerant** germplasm (Vadez *et al.*, 2007; Turner *et al.*, 2013)	• Increased seed yield under salinity not related to Na accumulation in the shoot	
Cowpea	Selection of **tolerant** cultivated germplasm (Chen *et al.*, 2007; Paul *et al.*, 2011)		
Lentil	Selection of **tolerant** cultivated and wild germplasm (Erskine *et al.*, 2011)		
Pea	Selection of **tolerant** germplasm (Shalid *et al.*, 2012)	• Osmotic adjustment	
Pigeon pea	Selection of **tolerant** wild germplasm (Upadhyaya *et al.*, 2013)		

(Continued on next page)

TABLE 1
Some of the major achievements in breeding for resistance to abiotic stress in legume crops with indication of potential inputs from knowledge on model legumes *(Continued)*

Species	Breeding Achievement	Traits Addressed	Potential Input from Model Legumes
			3) From *L.japonicus*: Identification of salt adapted genotypes (Sanchez *et al*., 2008; Rubio *et al.,* 2009)
Phosphorus, Iron and Boron deficiency			
Common bean	Selection of **low P tolerant** cultivated germplasm (Lynch & Beebe, 1995; Liao *et al*., 2004; Yan *et al*., 2004; Beebe *et al*., 2006, 2013a; Beebe 2012; Ramírez *et al*., 2013; Rao 2013)	• Root length, orientation, hair density (shallow roots) • Increased P use efficiency (PUE) • Enhanced photosynthate remobilization capacity	
Lentil	Selection of **Fe and B tolerant** cultivated germplasm (Erskine *et al*., 2011)		
Aluminum toxicity			
Alfalfa	Selection of **tolerant** genotypes or rhizobia strains tolerant to acid pH (Graham *et al*., 1994; Khu *et al.,* 2013; Reyno *et al*., 2013)	• Biomass production • Root growth associated with Al toxicity • Al translocation • Cell wall modifications • Isoflavonoid biosynthesis	**1) From *M. truncatula*:** Identification of novel genes associated with Al toxicity, resistance and tolerance (Chandran *et al*., 2008)
Common bean	Selection of **tolerant** cultivated and wild germplasm (Beebe 2012; Butare *et al*., 2012; Yang *et al*., 2013; Rao 2013)	• Citrate release • Vigorous root growth	
Pigeon pea	Selection of **tolerant** germplasm (Choudhary *et al*., 2011)	• Enhanced Al extrusion	
Heat			
Chickpea	Selection of **heat tolerant** cultivated germplasm (Krishnamurthy *et al*., 2011)	• Increased pollen germination under stress	
Cowpea	Selection of **heat tolerant** germplasm (Ehlers & Hall, 1997)	• Tolerant flower buds • Tolerance controlled by one dominant gene	
Cold			
Alfalfa	Selection of **cold tolerant** alfalfa genotypes (Cunningham *et al*., 1998; Justes *et al*., 2002; Castonguay *et al*., 2009; Remus-Borel *et al*., 2010)	• Higher autumn dormancy • Improved regrowth after winter • Differential remobilization of proteins to plant parts • Dehydrin accumulation	**1) From *M. truncatula*:** High-density genetic mapping revealed colinearity with a QTL related to freezing damage on *P. sativum* linkage group VI and syntenic markers were developed for transferability across 11 additional legume species (Avia *et al*., 2013; Tayeh *et al*., 2013a)
Cowpea	Selection of **cold tolerant** germplasm (Hall, 2004)	• Dehydrin accumulation	
Faba bean	Selection of **cold tolerant** cultivars (Arbaoui *et al*., 2008b; Hu *et al*., 2010; Link *et al*., 2010; Mikic *et al*., 2011)	• Winter hardiness	

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TABLE 1
Some of the major achievements in breeding for resistance to abiotic stress in legume crops with indication of potential inputs from knowledge on model legumes *(Continued)*

Species	Breeding Achievement	Traits Addressed	Potential Input from Model Legumes
Lentil	Selection of **frost tolerant** cultivated and wild germplasm (Eujayl *et al.*, 1999; Kahranan *et al.*, 2004a,b; Muehlbauer *et al.*, 2006; Erskine *et al.*, 2011)	• Winter hardiness	
Pea	Selection of **winter hardy** cultivar (Stoddard *et al.*, 2006; Lejeune-Hénaut *et al.*, 2008; Dumont *et al.*, 2009, 2011; Lucau-Donila *et al.*, 2012; Grimand *et al.*, 2013; Legrand *et al.*, 2013)	• Glucose and rafinose content, • RuBisCO activity • Higher chloroplast and chlorophyll content • Increased resistance to photoinhibition	

biochemical photosynthetic processes suggesting that plants are able to avoid leaf dehydration. On the other hand, under severe water deficit Ribulose-1,5-bisphosphate (RuBP) regeneration and Rubisco carboxylation efficiency were both decreased suggesting that non-stomatal limitations (Flexas and Medrano, 2002) also occurs in addition to mechanisms involving osmotic adjustment (Boyer and Meyer, 1979). Despite the findings previously described, further studies are needed to enhance our understanding of *M. truncatula* responses to water deprivation, including growth analyses, as well as, the characterization of accumulated osmolytes and the limitations in Rubisco carboxylation efficiency.

Soybean is the world's leading economic oilseed crop and vegetable protein for food and feed (Manavalan *et al.*, 2009). Moreover, soybean is also recognized as a model seed legume (Young and Bharti, 2012). Several studies performed on environmentally-controlled greenhouse conditions aimed to understand soybean physiological mechanisms activated by drought, with emphasis on flowering, pod abortion, pod expansion, seed yield and individual seed weight (Desclaux and Roumet, 1996; Desclaux *et al.*, 2000; Liu *et al.*, 2003, 2004). Soybean plants were exposed to several water deprivation schemes and water status, ABA contents in xylem sap, leaves, flowers and pods were measured at 0, 3, 5, 7, and 10 days after anthesis (DAA). Overall results suggested that drought-induced decrease in water potential and increase in ABA content in flowers and pods at critical developmental stages such as early reproductive development (3–5 DAA), contribute to pod abortion in soybean, thus compromising seed yield. Additionally, decrease of carbohydrate flux from leaves to pods, together with decreased hexose to sucrose ratio in pods are suggested as potential factors contributing to pod abortion in drought-stressed soybeans (Liu *et al.*, 2004).

Lotus japonicus, like *M. truncatula*, serves as a model for the study of several other species of the genus *Lotus*, that are widely used as pasture in temperate regions (Handberg and Stougaard, 1992; Betti *et al.*, 2012). Recent work evaluated the impact of water deficit stress in metabolism of reactive nitrogen and oxygen species (RNS and ROS, respectively) in *L. japonicus* (Signorelli *et al.*, 2013). The authors showed differential spatial distribution of oxidative and nitrosative stress as a consequence of the water deprivation imposed. The oxidative and the nitrosative stress component were higher in leaves and roots, respectively. Moreover, clear evidence of cross-talk between the different stress-signaling metabolites (proline or nitric oxide) measured were identified. Another study in *M. truncatula* demonstrated a cross-talk between H_2O_2 and NO signaling pathways in response to drought stress and rewatering, both at a local (root) and systemic (leaves) level (Filippou *et al.*, 2011). These studies are examples of the complexity underlying plant adaptation to drought, and the question of the existence of a truly specific abiotic stress signaling responses still remains unanswered (Knight and Knight, 2001).

The genetic and molecular basis of drought resistance in legumes has been deeply dissected via QTL or gene discovery approaches through linkage and association mapping mostly in soybean (Charlson *et al.*, 2009; Du *et al.*, 2009) and *M. truncatula* (Badri *et al.*, 2011; Vandecasteele *et al.*, 2011). A recombinant inbred population was developed from a cross between two contrasting soybean parental lines: Kefeng1, drought tolerant, and Nannong1138-2, drought sensitive (Du *et al.*, 2009) and used to measure multiple traits related to drought resistance and seed yield under water-stressed and well-watered conditions in field and greenhouse trials. A total of 40 QTLs were identified: 17 for leaf water status traits under drought stress and 23 for seed yield under well-watered and drought-stressed conditions in both field and greenhouse trials. Phenotypic correlations of traits studied suggested that several QTLs had pleiotropic or location-linked associations. Besides elucidating the genetic basis of drought tolerance, this study also provided the identification of reliable QTLs for drought resistance and improved seed yield to be incorporated into a marker-assisted selection breeding program aiming the development of high-yielding soybean cultivars with improved tolerance to drought stress (Scaboo *et al.*, 2009; Fallen *et al.*, 2013). Seed vigor, a measure of the quality and viability of the seed, is an important trait for successful seedling establishment under unfavorable environmental conditions (Maun, 1994). The raffinose oligosaccharide family (RFO) of soluble sugars plays a major role as an energy supply for legume seedling establishment, although its role in seed vigor is not well understood. Vandecasteele *et al.* (2011) investigated whether the composition or amount of soluble sugars (sucrose and RFO) was part of the genetic determinants of seed vigor in *M. truncatula* using two recombinant inbred line (RIL) populations. The correlation and co-location of Suc/RFO ratio with germination and radicle growth QTLs suggested that an increased Suc/RFO ratio in seeds might negatively affect seed vigor. These examples from model legumes may provide valuable information that could be utilized to implement a marker-assisted selection breeding program aimed at developing legume cultivars with improved tolerance to drought stress.

The stomatal limitation on photosynthesis imposed by the earlier stages of water deprivation leads to deprivation of carbon and therefore excess of photochemical capacity (Chaves, 1991). In other words, the quantity of light absorbed can easily exceed the capacity of the chloroplast for using the products of the photochemical reactions. If protection mechanisms are not activated, the excess of absorbed energy may induce photo-oxidative damage in chloroplast structures. To cope with such injuries, plants accumulate specific stress-associated proteins such as the Early-light Inducible Proteins (ELIPs). ELIPs and ELIP-like are nuclear encoded proteins and belong to the chlorophyll a/b-binding protein (cab) family (Adamska, 1997). Transgenic *M. truncatula* plants overexpressing the ELIP-like DSP22 protein display higher amount of chlorophyll (Chl), lower Chl a/Chl b ratio and higher actual efficiency of energy conversion in PSII after dehydration and rehydration, also suggesting a role in pigment stabilization during water deficit stress (Araújo *et al.*, 2013). The mechanisms by which DSP22 leads to enhanced photo-oxidative protection in *M. truncatula* are unclear, but the results support that the expression of photo-protective proteins, such as ELIPs, could be a useful approach to improve abiotic stress resistance in legumes.

The accumulation of osmoprotectants such as proline (Pro) is a common physiological response found in many plants grown in a wide range of biotic and abiotic stresses, including water deprivation (Yoshiba *et al.*, 1997; Verbruggen and Hermans, 2008). The proline biosynthetic pathway in plants is well known: L-Pro is synthesized from L-glutamic acid (L-Glu) via delta(1)-pyrroline-5-carboxylate (P5C) by two enzymes, P5C synthetase (P5CS) and P5C reductase (P5CR). Like many other similar metabolites, L-Pro can be metabolized to L-Glu via P5C by action of two enzymes: proline dehydrogenase (oxidase) (ProDH; EC 1.5.99.8) and P5C dehydrogenase (P5CDH; EC 1.5.1.12). Engineering the accumulation of Pro was used to increase drought resistance in plants, including legumes (De Ronde *et al.*, 2004; Simon-Sarkadi *et al.*, 2005; Kim and Nam, 2013). Transgenic soybean plants over expressing a cDNA coding for P5CR have enhanced accumulation of Pro and constituted an excellent platform to understand the role of Pro in conferring improved resistance to drought stress (De Ronde *et al.*, 2004). Moreover, manipulation of Pro content also affected the stress-induced changes in the concentration of several other amino acids, which further suggests the coordinated regulation of their metabolic pathways (Simon-Sarkadi *et al.*, 2005). In *M. truncatula*, the manipulation of the trehalose metabolism was shown to be a promising strategy to enhance resistance to imposed water deficit, including the recovery from severe water deficit (Duque *et al.*, 2013), and thus could be a valuable approach for plants to maximize the use of water from a brief rain period in the middle of a severe drought period.

The discovery of non-coding RNA (ncRNA) genes, which produce functional RNA molecules rather than encoding proteins, has undoubtedly changed our understanding of gene expression regulation in living organisms (Eddy, 2001). Among ncRNAs are the microRNAs (miRNAs) who play important regulatory roles, not only in plant development, but also in stress responses by negatively affecting target gene expression post-transcriptionally. A comprehensive description of the microRNA pathway in plants, including other short-interfering RNA, can be found in Bustos-Sanmamed *et al.* (2013). During the last decade, several miRNA involved in drought stress have been described for *M. truncatula* (Szittya *et al.*, 2008; Wang *et al.*, 2011), *G. max* (Li *et al.*, 2011), and for *L. japonicus* (Hu *et al.*, 2013). Trindade *et al.* (2010) analyzed the expression of several conserved miRNA in *M. truncatula* to investigate if miRNA-mediated regulation of gene expression was involved in responses to water deficit. They found that up-regulation of miR398a/b and miR408 correlates with down-regulation of their targets in water deficit. Interestingly, both miRNAs appear to modulate the expression of genes encoding copper proteins, suggesting a link between copper homeostasis and *M. truncatula* adaptation to progressive water deficit. Additionally, it has been also demonstrated that in *M. truncatula*, transcript accumulation of the components of small RNA pathways, such as Dicer-like Argonaute genes, is also modulated under water deficit (Capitão *et al.*, 2011). These studies demonstrated the involvement of transcriptional and post-transcriptional regulatory mechanisms mediated by small RNAs in drought stress response.

The multiple levels of complexity and cross-talk seen in legumes drought responses can benefit from the use of global System Biology to deeply understand the mechanisms involved (Jogaiah *et al.*, 2013). In *L. japonicus*, four days of water withholding induced an extensive reprogramming of the transcriptome from different metabolic pathways: photosynthesis, amino acid metabolism and cell wall metabolism, among others (Betti *et al.*, 2012). Besides elucidating the molecular mechanisms of stress response, genome-wide transcriptional analysis of two soybean genotypes under dehydration and rehydration conditions identified several drought-responsive genes to support further soybean breeding programs (Chen *et al.*, 2013). Several transcriptomics, proteomics and metabolomics approaches to understand seed development and grain filling have taken advantage of the genomic resources available for *M. truncatula* and *L. japonicus* (Gallardo *et al.*, 2007; Verdier *et al.,* 2008, 2013a, 2013 b; Dam *et al.*, 2009). To the best of our knowledge, none of the studies using the models mentioned above have been focused on the impact of drought stress on these developmental processes. Nevertheless, a very recent review reports the challenges and future prospects of soybean proteome to get new insights into the plant abiotic stress response mechanisms (Hossain *et al.*, 2013).

B. Salt Stress

Salt stress is one of the most significant environmental constraints limiting legume productivity in arid and semi-arid regions (Asraf and Harris, 2004; Hussain *et al.*, 2009). Soil salinity affects about 80 million hectares of arable lands worldwide (Munns and Tester, 2008). Salt stress is first perceived by the root system and impairs plant growth by inducing an osmotic stress caused by reduced water availability and from the ion toxicity due to solute imbalance in the cytosol (Munns, 2005; Conde *et al.*, 2011). This section focuses on salt stress constraints in the model species *M. truncatula*, *L. japonicus* and *G. max*. Several genotypes of *M. truncatula*, *L. japonicus* and soybean are adapted for growth in varying soil salt concentrations (Shao *et al.*, 1986; Kao *et al.*, 2006; de Lorenzo *et al.*, 2007; Phang *et al.*, 2008; Lazrek *et al.*, 2009; Ma *et al.*, 2010; Sanchez *et al.*, 2010, 2011; Sobhanian *et al.*, 2011; Zahaf *et al.*, 2012). These salt-adapted genotypes may contribute to understanding different mechanisms linked to salt stress.

Ion homeostasis is an essential factor of salt stress adaptation in salt-tolerant genotypes. In *M. truncatula*, the salt-tolerant TN1.11 genotype has increased root growth under saline conditions and accumulates more ions of both Na^+ and Cl^- in shoots than in roots, when compared to the reference Jemalong A17 genotype, which has moderate sensitivity to salt. This suggests a link between growth and ion transport (Zahaf *et al.*, 2012). In soybean, salt tolerance is partially explained by the compartmentalization of Na^+ into root cell vacuoles, preventing Na^+ transport to the leaves (Dabuxilatu and Ikeda, 2005; Luo *et al.*, 2005). An *et al.* (2002) also reported that Na^+ is retained in roots, whereas Cl^- is transported into leaves of both salt-tolerant Dare and salt-sensitive Tachiyutaka soybean genotypes. However, the differential transport of Na^+ and Cl^- ions in soybean roots and leaves may explain their response to salt stress. Selective mechanisms along the xylem-symplast boundary have been identified in soybean thus confirming the relationship between ion accumulation and salt tolerance (Sobhanian *et al.*, 2010). *L. japonicus* is also able to prevent Na^+ transport into shoots (Rubio *et al.*, 2009). Moreover, a comparative ionomic study of *L. japonicus* genotypes responding differentially to salt stress showed a strong correlation between shoot Cl^- levels of stress-acclimated genotypes and plant mortality exposed to lethal salinity doses (Sanchez *et al.*, 2011).

Overall, ion homeostasis is a complex process dependent on the specific genotype adaptation and the severity of the applied salt stress. As reported for other plant species, the K^+/Na^+ and Ca^{2+}/Na^+ ratios and uptake selectivity control discrimination between salt tolerant and salt sensitive legume genotypes (Phang *et al.*, 2008; Sanchez *et al.*, 2008). Furthermore, legume homologs of ion transporters were associated with salt stress responses and include Na^+ transporters and Na^+/H^+ antiporters (Phang *et al.*, 2008; Benedito *et al.*, 2010; Teakle *et al.*, 2010). Among them, the vacuolar Na^+/H^+ antiporter NHX1 (for Na^+/H^+ eXchanger) is involved in Na^+ compartmentalization (Li *et al.*, 2006; Zahran *et al.*, 2007; Teakle *et al.*, 2010). Several mechanisms of salt stress-tolerance involving osmoprotectants, ROS production, stress proteins and ion homeostasis in the three model legumes have been recently described (Table 2).

The global impact of salt stress, as well as the capacity to recover from the salt treatment was investigated in *M. truncatula* at the transcriptional level (Merchan *et al.*, 2007). In this study, 328 genes were linked to the recovery of root growth from a salt stress in the *M. truncatula* salt sensitive genotype R108. Among the genes found in this study was *MtZPT2-1*, a TFIIIA-like transcription factor shown to be involved in modulating root adaptation to salt stress (Merchan *et al.*, 2007). A comparative analysis of salt stress regulation in root apexes versus whole roots for the reference Jemalong A17 genotype was conducted using two complementary transcriptomic approaches; a massive quantitative real-time RT-PCR transcription factor profiling in whole roots and a Mt16K+ microarray analysis in root apexes. The results showed that 824 genes were differentially expressed when plants were subjected to early salt stress conditions, including 84 transcription factors. Interestingly, differential regulation of these transcription factors in root apexes were observed when compared to whole roots responses (Gruber *et al.*, 2009).

The development of the Affymetrix *Medicago* Gene Chip further expanded large-scale transcriptomic analysis for the evaluation of *Medicago* salt stress responses. To facilitate access to these gene expression profiles, an expression database called MtED, based on time-course salt experiments was developed (Li *et al.*, 2009). In addition, MtED was linked to the public resource MtGEA (*M. truncatula* Gene Expression Atlas, Benedito *et al.*, 2008), which includes the gene expression levels of different plant tissues.

Recent efforts to elucidate the stress tolerance mechanism to salt and saline-alkali stresses in soybean focused on a transcriptomic profiling analysis of seedling roots and leaves performed using high-throughput Illumina sequencing technology of the salt stress tolerant line HJ-1. The whole plant transcriptomic profile approach identified stress-regulated genes that were more up-regulated in roots than in leaves. The genes involved in stress signaling and transcription factors represented the most abundant categories expressed in response to these stresses (Fan *et al.*, 2013).

TABLE 2
Recent references describing major elements concerned in different salt stress tolerance mechanisms in model legumes

	Medicago truncatula	*Glycine max*	*Lotus japonicus*
Osmoprotectants	**Amino acids:** proline (Armengaud *et al.*, 2004) **Sugars and polyols:** trehalose (Lopez *et al.*, 2008)	**Amino acids:** proline (Aghaei *et al.*, 2008) **Sugars and polyols:** pinitol (reviewed in Phang *et al.*, 2008) **Dimethyl sulfonium compounds:** glycinebetaine (reviewed in Phang *et al.*, 2008) **Alkaloids:** trigonelline (reviewed in Phang *et al.*, 2008)	**Amino acids:** proline (Sanchez *et al.*, 2008; Rubio *et al.*, 2009), Serine and Asparagine (Sanchez *et al.*, 2008) **Organic acids:** glutamic, succinis, citric, malic, malonic, threonic acids (Sanchez *et al.*, 2008) **Sugars and polyols:** maltose, ononitol, pinitol, arabitol, erythritol (Sanchez *et al.*, 2008)
Reactive oxygen scavengers	**Antioxidant enzymes:** superoxide dismutase, total peroxidase, glutathione reductase, ascorbate peroxidise, guaicacol peroxidise (Bianco and Defez, 2009; Kang *et al.*, 2010; Mhadhbi *et al.*, 2011)	**Antioxidant enzymes:** superoxide dismutase, ascorbate peroxidise, Glutathione reductase (reviewed in Sobhanian *et al.*, 2011) **Non-enzymatic ROS scavengers:** ascorbic acid, carotenoid and glutathione (reviewed in Sobhanian *et al.*, 2011)	**Antioxidant enzymes:** superoxide dismutase, catalase, glutathione peroxydase and ascorbate-glutathione cycle enzymes (Rubio *et al.*, 2009)
Stress proteins	**LEA** (Late Embryogenesis Abundant) **proteins** (Soares-Cavalcanti *et al.*, 2012)	**LEA proteins:** group 1 (Soares-Cavalcanti *et al.*, 2012), groups 3 and 4 (reviewed in Phang *et al.*, 2008)	**LEA proteins** (Sanchez *et al.*, 2008)
Ion/proton transporters	**Na$^+$ transporters** (MtNHX1, MtNHX3 and MtNHX4 [Zahran *et al.*, 2007]), Na+/H+ antiporter (Kang *et al.*, 2010) **SOS-mediated signalling pathways:** SOS1 (Salt Overly Sensitive, Elmaghrabi *et al.*, 2013), SOS2 (Kang *et al.*, 2010)	**Na$^+$ transporters:** GmNHX1 Vacuolar Na+/H+ (reviewed in Phang *et al.*, 2008) H+-PPiase (GmVP1), H+-ATPase (GmVHA-C), Inward-rectifying K+ channel (GmAKT1), Vacuolar CLC chloride channel (GmCLC1), Cyclic nucleotide-gated cation channel (GmCNGC), Glutamate receptor (GmGLR3), Na+/K+/Cl− co-transporter (GmNKCC), Cation/proton exchanger (GmCAX1, [reviewed in Phang *et al.*, 2008]) **SOS-mediated signalling pathways:** GmSOS1 Na+/H+ antiporter (Phang *et al.*, 2008)	**Putative K+ transporter** (chr5.CM0911.54.1) and putative chloride channel (Ljwgs_016759.2, [Sanchez *et al.*, 2008])

In *L. japonicus*, 912 differentially expressed genes responding in a dose-dependent manner during salt acclimatization were identified using the Affymetrix *Lotus* GeneChip® Genome Array in the glycophyte *L. japonicus* var. Gifu (Sanchez *et al.*, 2008). To test the robustness of these data, experiments were performed during two consecutive years and around 30% of the transcriptional responses to salt stress were not reproducible in the second year. This highlights the difficulty to control the complex nutritional or environmental factors, even in greenhouse conditions present during stress responses (Sanchez *et al.*, 2010).

A complementary strategy to understand salt stress adaptation consists of comparing legume genotypes displaying contrasting physiological salt stress responses. Several salt-stress related genes were shown to be more highly expressed in roots of tolerant vs. sensitive *M. truncatula* genotypes (Jemalong A17 vs. R108, respectively) even in the absence of stress, linking these genes with genotype-specific regulatory pathways involved in salt stress responses (De Lorenzo *et al.*, 2007). Recently, a comparison between the salt-adapted TN1.11 and the reference Jemalong A17 *M. truncatula* genotypes was performed using a transcriptomic approach allowing the detection of important variations in root apex expression profiles in response to salt. The authors also found that a basic Helix-Loop-Helix transcription factor (Mt*bHLH–658*), was differentially regulated only in the tolerant genotype and increased adaptation of root growth to salt stress. De-regulation of this pathway under salinity conditions may explain the naturally diverging responses to salt stress of these genotypes (Zahaf *et al.*, 2012). This Mt*bHLH–658* may be a gene associated with salt stress adaptation of the TN1.11 tolerant genotype.

In soybean roots, a digital gene expression profile experiment highlighted a higher ratio of up/down-regulated genes in the salt-tolerant *G. soja* than in a salt-sensitive genotype of *G. max* (Ali *et al.*, 2012). In this study, 490 salt-responsive genes involved in the control of different steps of the salt regulatory pathway including many transcription factors were identified.

In addition, in *L. japonicus*, transcriptomic analysis of contrasting salt-tolerant model and cultivated species indicated that less than 1% of the transcriptional responses to salinity were found in all genotypes. The majority of these responses were unique to single or a few genotypes demonstrating the importance of genotype-specific transcriptional changes observed in salt stress adaptation (Sanchez *et al.*, 2011).

An integrated view of the salt tolerance mechanisms in legumes has benefited from other -omics approaches, including proteomic and metabolomics, that were recently developed to better understand the salt tolerance mechanisms (Aghaei *et al.*, 2008; Sobhanian *et al.*, 2010, 2011; Sanchez *et al.*, 2011; Xu *et al.*, 2011; Hakeem *et al.*, 2012). Growing evidence showed that transcription factors are key regulators of the plant responses relevant in salt stress adaptation (as exemplified in Merchan *et al.*, 2003; Chen *et al.*, 2007; Udvardi *et al.*, 2007; Liao *et al.*, 2008; Zhou *et al.*, 2008; de Lorenzo *et al.*, 2009; Pinheiro *et al.*, 2009; Wei *et al.*, 2009; Ariel *et al.*, 2010; Zhang *et al.*, 2010; de Zélicourt *et al.*, 2012; Cheng *et al.*, 2013; Zhai *et al.*, 2013). Recent studies pointed out that the expression of certain salt-responding transcription factors may be controlled by epigenetic changes (for example DNA methylation and/or histone modifications), modulating soybean tolerance to salt stress (Song *et al.*, 2012).

The use of QTL mapping for salinity tolerance based on recombinant inbred lines (RILs) generated from contrasting parental salt-responding genotypes was used to understand genotype-specific stress responses and to generate stress-tolerant plants for breeding programs. In a *M. truncatula* RIL population (Jemalong A17×F83005.5), putative QTLs associated with the response of leaves, stem and roots to Na+ and K+ uptake traits under control and salt-stress treatments, were mapped to several genomic regions (Arraouadi *et al.*, 2012). In soybean, major salt tolerance QTLs were identified and shown to be conserved between wild and cultivated species (Lee *et al.*, 2004; Hamwieh and Xu, 2008). Salt tolerance phenotypes seem to be dominated by major loci further suggesting the appearance of major genotype-specific mechanisms dealing with the adaptation of legumes to saline growing conditions.

In conclusion, the mechanisms involved in salt stress are complex although major advances have been achieved through genome sequencing and transcriptomics. The use of -omic approaches provide further insight into the regulation of salt tolerance in legumes. Several regulatory networks leading to salt stress adaptation seem genotype-specific and there may not be unique strategies in legumes used to cope with such a complex stress. Combination of QTL approaches associated with salt tolerance and genomics will contribute to understanding the diversity of mechanisms involved in salt stress responses and possibly result in novel candidate genes that could be useful for breeding programs.

C. Cold Stress

Plants are grouped into two broad categories based on their level of sensitivity to sub-optimal temperatures. Some are sensitive to temperatures ranging from 0 to −15°C (chilling stress), while others are capable of withstanding freezing temperatures. The first case corresponds to species native to tropical and subtropical regions. Species of temperate and cold regions belong to the second category. The degree of cold tolerance is variable among species and the freezing tolerance generally increases after exposure to cold and non-freezing temperatures. The response to cold exposure conducive to an increased freezing tolerance is often referred to as 'cold acclimation.'

The levels of cold tolerance are different between the galegoid clade (including *M. truncatula* and *L. japonicus*) and those in the phaseoloid clade (that includes *G. max*) reflect their geographical origins. Species of the galegoid clade are often described as cold and freezing tolerant while the phaseoloid species are considered cold and freezing sensitive.

Regarding the response to cold, most of the studies on model legumes were performed on *M. truncatula*. There are only two reports on chilling effects in *L. japonicus* seedlings: the down regulation of a long-chain fatty alcohol oxidase (LjFAO1) in the apex and the cotyledons of seedlings at 4°C (Zhao *et al.*, 2008) and the induction in seedlings of a non-symbiotic hemoglobin (Shimoda *et al.*, 2005) were identified.

Experiments on cold acclimation and freezing tolerance in *M. truncatula* are mostly limited to controlled conditions (Bounejmate *et al.*, 1994; Brandsæter *et al.*, 2000; Antolin *et al.*, 2005; Hekneby *et al.*, 2006; Pennycooke *et al.*, 2008; Thapa *et al.*, 2008; Zhang *et al.*, 2011; Avia *et al.*, 2013). Antolin *et al.* (2005) studied growth, net photosynthesis rate and chlorophyll fluorescence induction kinetics among annual legumes including *M. truncatula* cv. Paraggio under cold acclimation (10/5°C) and non-acclimation (20/15°C) regimes. Growth at such low temperature resulted in a 2-fold increase in stem and root dry matter without any changes in leaf dry matter, when compared with the ones growing at 20°C. The resulting photosynthetic cold acclimation was associated with a two-fold increase of quantum yield of photosystem II electron transport, pigment content, and in the activity of stromal fructose-1, 6-bis-phosphatase (sF-BPase). Hekneby *et al.* (2006) compared growth parameters, proline, starch and sugar contents and regrowth capacity after a freezing treatment in the same accession. The root:shoot ratio increased in the cold-treated cv. Paraggio, but the total dry matter, leaf area, specific leaf area did not differ between the two applied temperature treatments (10/5°C vs. 20/15°C). In the same study, increased levels of soluble sugars and proline were also observed, as well as lower ice nucleation temperature and lower LT_{50} (lethal temperature of 50% of the population). The authors concluded that *M. truncatula* genotypes had an ineffective cold acclimation process because of impaired sucrose phosphate synthase (SPS) activity in leaves and low starch reserves in roots which resulted in poor regrowth of the cultivar. This is in agreement with the results of another study, in which *M. truncatula* cv. Parabinga exhibited one of the poorest levels of frost tolerance in legumes after an acclimation at 2°C for 2 weeks (Brandsaeter *et al.*, 2000). Additionally, these authors suggested that the poor survival of the plants could be related to the fact that they had already initiated flowering when cold temperatures were induced in the growth chamber.

Divergent cold responses have been described for the cultivar Jemalong (A17) across different experiments. For this accession, Zhang *et al.* (2011) observed increased levels of sucrose, fructose, lactose, proline, osmolality, survival rates and a decrease in EL_{50} (temperature that kills 50% of tissues due to electrolyte leakage) after a cold exposure at 4°C. Alternatively, Pennycooke *et al.* (2008) did not find any significant improvement in the freezing tolerance for this Jemalong cultivar, after cold exposure at 2°C. This contrasted behavior for the same genotype could be due to differences in the age of the seedlings (three and four weeks in the first and the latter study, respectively) or in the temperature and length of exposure utilized during acclimation. Two other accessions, namely W6 5018 and Jemalong-6, had an increased ability to improve their frost tolerance following the exposure to a three-step acclimation program (10/5°C, 7/4°C, 3.5/$-$1°C) as evidenced by a significant decrease in LT_{50} (Thapa *et al.*, 2008). In these experiments, the LT_{50} was the freeze temperature at which 50% injury occurs and injury was estimated using the electrolyte leakage or EL method. Recently, 15 lines from different geographical origins, including Jemalong, revealed natural variation for freezing tolerance evaluated by freezing damage and EL after cold exposure in a two-step program (12/12°, 8/2°C) (Avia *et al.*, 2013). The accessions originating from lower latitudes (Algeria, Cyprus, and Syria) were found to be more sensitive than those from France. However, no clear relationship was found between freezing tolerance and the altitude of the area of origin. In general, it seems that some *M. truncatula* genotypes have the ability to cold acclimate better than others when exposed to a gradual decrease in temperatures.

Regions of the *M. truncatula* genome determining variation for freezing tolerance have been identified using a QTL mapping approach (Avia *et al.*, 2013) to identify three QTLs located on chromosomes 1, 4, and 6. A major freezing tolerance QTL (Mt-FTQTL6) accounting for 40% of the phenotypic variation was mapped to a region of *M. truncatula* chromosome 6 coinciding with an assembly gap in the Jemalong A17 euchromatic in the version Mt3.0 of the genome assembly (Tayeh *et al.*, 2013a). A high-density genetic map of the Mt-FTQTL6 revealed colinearity with a QTL related to freezing damage on pea (*Pisum sativum*) linkage group VI and syntenic markers were developed for transferability across 11 additional legume species (Tayeh *et al.*, 2013a). These cross-legume markers will be useful in future efforts aimed at investigating the conservation of Mt-FTQTL6 in cool-season legumes and subsequently the existence of common mechanisms for response to freezing shared between *M. truncatula* and crop legumes.

At the molecular level, the *M. truncatula* freezing tolerance response has been studied through the expression of the CBF/DREB1 gene family. This is a small family of transcriptional activators binding to the C-repeat/dehydration-responsive element, which is present in the promoters of many cold-responsive genes. To date, four CBF genes have been identified and studied in *M. truncatula*, namely MtCBF1-4 (Pennycooke *et al.*, 2008; Zhang *et al.*, 2010; Li *et al.*, 2011). *MtCBF2* and *MtCBF3* were found to be rapidly induced under low temperatures (Pennycooke *et al.*, 2008; Zhang *et al.*, 2011). A transient increase of *MtCBF1* transcripts has also been observed under these conditions (Zhang *et al.*, 2011). Transformation of *M. truncatula* for overexpression of *MtDREB1C*, identical to MtCBF3, suppressed shoot growth, and enhanced freezing tolerance (Chen *et al.*, 2010). *MtCBF4*, isolated during osmotic stress experiments was induced in *M. truncatula* during cold stress (Li *et al.*, 2009). The expression of CBFs seems to induce the expression of effector genes such *MtCAS15* and *MtCAS31* (*M. truncatula* cold acclimation-specific 15 and 31) containing *cis* CRT/DRE elements (Pennycooke *et al.*, 2008). For example, over-expression of *MtCBF4* in transgenic *M. truncatula* improved cold tolerance (4°C) and activated expression of downstream genes containing the DRE elements *MtCAS15* and *MtCAS31* (Li *et al.*, 2011). The MtCAS31 protein is a dehydrin isolated during osmotic stress experiment (Li *et al.*, 2009) which was also expressed during cold exposure (4°C) in *M. truncatula* (Xie *et al.*, 2012). MtCAS31 protein expressed in transgenic Arabidopsis interacted with *Arabidopsis thaliana* inducer of CBF expression 1 protein (Xie *et al.*, 2012) which is an up-regulator of the expression of CBF3 (reviewed by Medina *et al.*, 2011). These results confirm the crucial role of these genes in the cold-response regulatory pathway. Recently, twelve *CBF/DREB1* genes including 10 new sequences in *M. truncatula* were identified and localized to

Mt-FTQTL6 (Tayeh *et al.*, 2013b). They revealed unique features characterizing *CBF/DREB1* genes such as alternative splicing and large tandem duplication.

Other transcription factors are known to be expressed in response to 4°C treatment in *M. truncatula* roots: DOF207, HD1374, MYB634, MYB636, MYB1070, NAC969, NAC1081 and NAC1126 (Gruber *et al.*, 2009) and AP2-like transcription factors, *MtZpt2-1*, *MtZpt2-2*, *MtAp2*, and a salt-induced receptor-like kinase *MtSrlk* (Merchan *et al.*, 2007). These genes are also expressed during osmotic and heat stresses (Gruber *et al.*, 2009) or salt stresses (Merchan *et al.*, 2007). Transgenic plants of Arabidopsis that constitutively expressed *MtHB2* (transcription factor belonging to the HD-Zip II subfamily) were more sensitive to freezing stress than wild-type plants. Expression of *MtHB2* in *Arabidopsis* revealed that the transgenic plants accumulated lower amounts of proline and soluble sugars and greater amounts of malondialdehyde and H_2O_2 than their wild-type counterparts grown with and without abiotic stresses. The osmoregulation observed in transgenic plants was less effective and plants were more susceptible to oxidative damage under the conditions of cold stress. This demonstrated that *MtHB2* likely plays a negative role in regulating cold stress responses (Song *et al*., 2012).These studies focused on the effects of cold acclimation in heterotrophic seedling growth.

During crop establishment, cold can decrease plant germination and heterotrophic growth and lead to drastic losses in crop yield and quality. QTL for seed mass in *M. truncatula* (chromosomes 5 and 8), germination (chromosomes 3 and 8) and heterotrophic growth (chromosomes 1, 2, and 8) were found at sub-optimal temperatures (Barreto Dias *et al.*, 2011). Based on data mining approaches, these authors also identified a set of putative candidate genes already identified during cold stress and involved in membrane protection and repair (LEA like proteins, HSP70 proteins) or those involved in regulation (RD22, ZAT10, ICE1, CBF1, CSDP1, OBF4). *MtSAP1* (*M. truncatula* stress-associated protein 1) a protein with A20 and AN1 zinc-finger domains was necessary to achieve successful germination and was induced in the embryo axis during acquisition of tolerance to desiccation and cold stress (Gimeno-Gilles *et al.*, 2011). Compared to wild type, tobacco plants over-expressing *MtSAP1* were less affected in their growth and development at 4°C which confirms the involvement of this gene in the response of cold stress (Charrier *et al.*, 2013).

Medicago truncatula shows genetic variability for cold acclimation and freezing tolerance. The responses of this species to cold stress are sometimes common with those to drought, heat and osmotic stress, suggesting cross-talk between these abiotic stress responses. CBF genes are involved in freezing tolerance in *M. truncatula* although the details of their regulation remain unknown. Recent results have demonstrated syntenic relationships between QTL for frost tolerance in *M. truncatula* and *P. sativum* which highlights the potential benefit of using this model species to help decipher the determinism of cold tolerance among cultivated legumes.

D. Symbiosis under Abiotic Stress

Legume plants are able to establish intimate symbiosis with N_2-fixing soil bacteria collectively referred to as rhizobia. This symbiotic interaction results in the formation of a unique organ, the nodule, where atmospheric N_2 is reduced to ammonium in a differentiated form of the rhizobium bacteria (bacteroids) via symbiotic nitrogen fixation (SNF). This reduced N is exported from the nodule to the whole plant, so that the plant obtains a source of nitrogen and the bacteria is provided with photoassimilates in exchange.

For a successful symbiosis interaction to occur, the environmental requirements of both partners should be fulfilled. Any abiotic stress that alters soil conditions, such as drought, high temperature, salt or soil acidity, also affects the soil microbial community, thus compromising the symbiotic interaction (Tate, 2000). In general, rhizobia are more tolerant than their respective plant host to stress (Zahran, 1999), exhibiting different coping strategies including osmoregulation and homeostasis maintenance processes (Ghittoni and Bueno, 1996; Priefer *et al.*, 2001). For instance, Dominguez-Ferreras *et al.* (2009a, b) showed the importance of potassium uptake and trehalose metabolism for *Sinorhizobium meliloti* osmotolerance. Other responses such as modification of cell morphology or extracellular polysaccharides pattern have been also observed (Vriezen *et al.*, 2007). The role of the microsymbiont conferring stress tolerance to the host has been shown for *Sinorhizobium* strains overproducing cytokines (Xu *et al.*, 2012). However, the tolerance of the legume host highly determines the effectiveness of the symbiotic interaction under stress conditions (Craig *et al.*, 1991; Zahram, 1999). The different stages of the plant-bacteria interaction, root hair curling, bacterial colonization, infection thread formation and nodule development are highly reduced under stress conditions, influencing the success of the SNF process (Zahran and Sprent, 1986).

Reduction in the rate of SNF was described in both model (Larrainzar *et al.*, 2007, 2009; Lopez-Gómez *et al.*, 2011; Gil-Quintana *et al.*, 2013a) and crop legumes (González *et al.*, 1995, 1998; Ramos *et al.*, 1999; Gil-Quintana *et al.*, 2013b; Palma *et al.*, 2013) when exposed to drought and salt stresses. In this context, it is worth noting that studies on *L. japonicus*, the genetic model for determinate nodule-forming legumes, are scarce and the state of the art is mainly based on pea, soybean, common bean (*Phaseolus vulgaris*) and *M. truncatula*.

Despite considerable research efforts, the molecular mechanism(s) responsible for the inhibition of SNF remain largely unknown. The complexity of the SNF process and the particular environment where it occurs, increase the number of possible factors altering this process under abiotic stress. Among them, several inhibiting factors have been proposed and these include oxygen limitation, carbon shortage, and regulation by nitrogen metabolism. Although drought, similarly to other abiotic stresses, does cause an increase in nodular oxygen diffusion resistance (Durand *et al.*, 1987), increasing the oxygen concentration around the rhizosphere of drought-stressed nodules does not fully restore SNF rates, suggesting that other factors may be involved (Del Castillo *et al*., 1994, 1995). Several studies performed in grain legumes (i.e., pea, soybean, common bean) subjected to drought showed that the reduction of SNF rates was related to a concurrent inhibition of sucrose synthase activity, followed by an accumulation of sucrose and a decrease in malate to fuel bacteroid respiration (Gonzalez *et al*., 1995, 1998; Gordon *et al*., 1997; Ramos *et al*., 1999). Nevertheless, a different cause was suggested for the forage legume alfalfa (*Medicago sativa*) (Naya *et al*., 2007) and *M. truncatula* (Larrainzar *et al*., 2007, 2009), since SNF inhibition occurred before any measurable decline in either the activity rate or concentration of nodule carbon metabolism enzymes. In this regard, the level of malate did not show significant changes in these forage legumes (Naya *et al*., 2007; Larrainzar *et al*., 2009), suggesting that a different regulatory mechanism may be taking place in forage vs. grain legumes. In this sense, a large accumulation of amino acids was originally observed in *M. sativa* exposed to salt-stress (Fougere *et al.*, 1991) and, more recently, Lopez-Gomez *et al*. (2011) identified several nodule osmoprotectors with a putative role on salt stress in *L. japonicus* compared to *M. truncatula*. In leaves of model and forage legumes of the *Lotus* genus, Sanchez *et al*. (2012) noted the high diversity of responses occurring among the different species and partial similarities between the salt- and drought-responsive metabolites. Nevertheless, information is still limited and further studies are needed to fully understand the role of carbon metabolism on SNF regulation in the different model and crop legumes.

The N status of the whole plant was also proposed as a factor regulating SNF via a feedback inhibition of nitrogenase activity. The hypothesis of a N-driven regulation of SNF during drought stress has received much attention in tropical legume research, mostly due to studies in soybean, where the accumulation of N compounds such as ureides, and the amino acids Asn and Asp in different plant organs has been reported (Serraj *et al.*, 1999; Vadez *et al.*, 2000). Serraj *et al*. (2001) refined this model further by proposing two possible origins for this feedback inhibition: (i) a direct feedback inhibition within nodules, and (ii) an indirect feedback process due to N signals coming from the aerial part. However, for many years, this last hypothesis has only been formally tested in ureide-exporter legumes, but not in amide-exporters. In a recent study, Gil-Quintana *et al*. (2013a) challenged the N-feedback hypothesis in the amide-exporter legume, *M. truncatula* when it was subjected to drought stress implemented using a split root system. This study showed that the regulation of SNF during drought occurs at the local level, similarly to the case of pea (Marino *et al.*, 2007) and soybean (Gil-Quintana *et al.*, 2013b). In these three species, SNF declines exclusively in nodules from the water-stressed part of the root, whilst nodules on the well-watered root portion did not display stress symptoms, thus supporting a local regulation system. Also, the concept of a N-signal coming from individual amino acids, acting as N-feedback inhibitors was tested. When the pattern of accumulation of single amino acids in different plant tissues was compared, the conclusion was that a more intricate regulation of N metabolism actually occurs. Indeed, the observed amino acid accumulation in roots and nodules, regardless of SNF rates, appears to be a general drought stress response that cannot be directly related to SNF. In agreement with these observations, ureide accumulation was recently shown to be induced by changes of ureide metabolic enzymes in drought-stressed soybean (Gil-Quintana *et al.*, 2013b).Ureide accumulation was also observed in non-fixing plants (Alamillo *et al.*, 2010) suggesting a constitutive response to drought stress and thus, not exclusive of nodulated legumes. Accumulation of N compounds occurring in different tissues may respond to the inhibition of protein synthesis of water-stressed tissues, as previously reported (Hsiao, 1973; Good and Zaplachinski, 1994), yet poorly investigated. Another unresolved question is how stress affects the vascular interactions between roots and nodules, a subject that has raised speculation (Pate *et al.*, 1969), and that requires further testing. Interestingly, a transcription factor related to salt tolerance has been recently shown to have a dual involvement in root and nodules with antagonistic response (de Zelicourt *et al.*, 2012), suggesting common regulatory mechanisms in both organs.

In summary, future research on the molecular mechanism(s) responsible for the inhibition of SNF should focus on the nodule environment and the regulatory role initially given to N compounds accumulated under stress conditions needs to be further evaluated. Additionally, information on SNF regulation coming from the temperate model legume *M. truncatula* may be more applicable to other forage legumes, regardless of their origin, than to grain legumes, even if their origin is from a similar geographical zone.

III. ABIOTIC STRESS RESPONSE OF LEGUME CROPS

Legume improvement should focus on a myriad of challenges for grain legumes and forages, namely concerning improvement towards abiotic stress resistance or tolerance. Common bean, chickpea (*Cicer arietinum*), pea and faba bean (*Vicia faba*) are some examples of the most cultivated staple food legumes for direct human consumption in the world. Soybean is the world's leading economic oilseed crop and vegetable protein for food and feed (Manavalan *et al*., 2009). However, due to its characteristics and genomic or genetic resources available, it is now rightly considered as well a model species (Cannon, 2013) and thus it was addressed on the previous model legume section. Others, such as cowpea (*Vigna unguiculata*), pigeon pea (*Cajanus cajan*), lentil (*Lens culinaris*), and grass pea (*Lathyrus sativus*) also have also an important role as staple crops mainly in some of the most marginal and harsh regions of the world. Our review will focus not only on the achievements and prospects for the above mentioned crops, but also on forage legumes belonging to the *Medicago*, *Trifolium* and *Lotus* genera, since they are essential components of livestock production in agricultural systems. Although model legumes have provided valuable tools and knowledge to understand legume adaptation to harsh environments, the challenge to transfer this information for the benefit of crops or forages grown under field conditions remains (Deikman *et al.*, 2012).

A. Common Bean

Common bean is the grain legume for direct human consumption with the greatest total production in the world, estimated at around 12 million tons per year, mainly in Latin America and Africa (Beebe, 2012). Like other legumes, beans are a source of protein, complex carbohydrates, fiber, minerals and folate. Yields of common bean are severely limited by abiotic stress, especially climate-related and soil-related constraints (Rao, 2014). This review section will consider aspects of common bean response to different stresses, and will suggest an ideotype with a combination of desirable traits to deal more effectively with the unpredictability of abiotic stress, and with possible interactions among stresses.

1. Abiotic stress responses

a. Drought. Mechanisms by which plants resist drought include: dehydration avoidance and desiccation tolerance (Beebe *et al.*, 2013b). Resistance to severe drought can be critical in natural dryland ecosystems, but has little relevance to increasing or stabilizing crop productivity. Increasing crop yield in drought-prone areas requires the optimization of the physiological processes involved in plant response to soil water deficit. Dehydration avoidance mechanisms serve to ameliorate the effects of drought by reducing either the water deficit or the crop's exposure to it, and are defined as the plant's ability to maintain its water status under conditions of soil water deficit. Early maturity is the most common escape mechanism, and cultivars with this strategy are favored by many farmers, at least in part to minimize exposure to terminal drought (White and Singh, 1991), as with the extra early common bean cultivar 'ICTA Ligero' in Guatemala. However, each day of reduced growth cycle was estimated to reduce yield potential by 74 kg ha^{-1} (White and Singh, 1991).

Superior drought performance of genotypes BAT 477 and San Cristobal was attributed to an avoidance mechanism that involves deeper rooting in response to soil drying (Sponchiado *et al.*, 1989). A grafting experiment in which shoots and roots of susceptible and resistant genotypes were interchanged confirmed that resistance was attributed to the roots (White and Castillo, 1992). QTL for this trait, as expressed in a greenhouse soil tube method, were identified but did not correspond to QTL for yield under field conditions with moisture deficit (Asfaw and Blair, 2012). A dehydration avoidance mechanism is also reflected in stomatal control, whereby the crop reduces its evapotranspiration during its vegetative phase, thus conserving moisture for the grain filling period. This mechanism was recognized in soybean (Sinclair *et al.*, 2000; Sinclair, 2012) and initial studies in a greenhouse trial revealed a similar trait in elite common bean lines resulting from the drought selection (Devi *et al.*, 2013).

Desiccation tolerance and water use efficiency (WUE) are likely to be very different from escape or avoidance mechanisms and thus require different strategies to elucidate and utilize them. Similarly, induced mechanisms must be treated differently from constitutive mechanisms. WUE is the ratio of total dry matter to evapo-transpiration and other losses of water from the system that is not transpired through the plant. An increase in transpiration efficiency (TE; defined as the ratio of accumulated plant mass to water transpired) or a reduction in soil evaporation will increase WUE (Blum, 2010). However the real challenge is to increase the effective use of water for transpiration when water is limiting (Blum, 2009). Sinclair (2012) concluded that TE is not a variable that can be easily resolved for use in many breeding programs. He suggested that component traits contributing to TE need to be studied to increase the effective use of available water through the growing season. High TE is obtained by partial stomatal closure, and consequently by a decrease of transpiration that could lead to lower crop yields. Developments in infrared thermography could provide new and feasible screening methods for detecting genetic variation in the stomatal response to water deficit in controlled environments and in the field (Munns *et al.*, 2010).

Breeding for drought resistance in common bean has been based on measuring yield under drought conditions and this approach has been successful in enhancing crop productivity under drought stress (see Beebe *et al.*, 2013b for a review). Most progress has occurred within the Middle American gene pool, and has resulted from combining the small seeded race Mesoamerica with the Durango race originating from the dry highlands of Mexico. Lines with superior drought yield in Colombia display better remobilization of photosynthate to pod formation and to grain during the grain filling period (Beebe *et al.*, 2008; Rao *et al.*, 2009; Beebe *et al.*, 2013b; Rao *et al.*, 2013). This resulted in greater harvest index (HI), and this result is consistent with other studies reporting that maintenance of HI under drought is key to drought resistance (Ramirez-Vallejo and Kelly, 1998; Klaedtke *et al.*, 2012; Habibi, 2013). This trait could be particularly important during terminal drought as a desiccation tolerance mechanism when stress becomes increasingly acute at the end of the season. It is a trait with wide utility under multiple patterns of drought, in shallower soils of hillsides agroecosystems with limited potential for deep rooting, under other types of stress and even under optimal conditions (Beebe *et al.*, 2008, 2013a, b; Beebe, 2012). Pod harvest index (PHI; seed weight / total pod weight x 100) has been employed as an indicator of photosynthate remobilization capacity under stress (Rao *et al.*, 2013). Assefa *et al.* (2013) found that under drought, PHI had higher heritability than yield under drought, and that selection for PHI would result in greater genetic gain than direct selection for drought yield, and would also enhance non-stressed yield. This was consistent with results of Beebe *et al.* (2008) who found superior yield potential under favorable conditions among drought selected lines. These results were interpreted in the context of correcting deficiencies inherited from the wild ancestor that likely addressed intermittent drought by repressing its reproductive development until rainfall resumed. Selection for greater pod set and grain filling under drought serves to reverse this ancestral tendency and to identify genotypes with better partitioning to reproductive structures. Multienvironment QTL analysis for photosynthate remobilization traits under drought stress indicated that QTL for grain yield and photosynthate remobilization traits were independent of QTL for rooting depth or rooting pattern in a RIL population derived from BAT 477 and DOR 364 (Asfaw and Blair, 2012; Asfaw *et al*., 2012). Genotypes that could combine earliness, deep rooting and photosynthate mobilization could be more resilient for use in smallholder farm conditions minimizing risk from climate change and low soil fertility.

Tepary bean (*Phaseolus acutifolius*) evolved under a very different environment than the common bean. In contrast to wild *P. vulgaris* that had to compete for light with shrubs and weedy species, light is abundant in the desert environments where *P. acutifolius* evolved. Clearly, water is the most limiting factor in these environments. Tepary bean exhibits several drought resistance traits: early maturity, excellent remobilization capacity under stress, deep rooting to avoid dehydration, small leaves for reduced water use, and stomatal control but not with osmotic adjustment (Mohamed *et al*., 2005). This suggests that superior adaptation to drought can result from the combination of multiple traits, and in this sense tepary may serve as a model for improvement of drought resistance in common bean (Rao *et al*., 2013). Such traits may be sought within common bean germplasm, or they may be introduced from tepary through interspecific crosses. A reserve of tepary by common bean hybrid progenies exist (Mejía-Jiménez *et al.*, 1994; Muñoz *et al.*, 2004) and these may be explored for genes contributing to drought resistance.

b. Heat. Beans are grown across a wide range of latitudes with mean air temperature of 14°C to 35°C. The Andean gene pool typically adapts best at mid-high altitudes (1400-2800 masl) or cooler climates, with race 'Nueva Granada' being more heat tolerant than race 'Peru'. The Mesoamerican gene pool adapts to higher temperatures at low (400 masl) to mid-high altitudes (2000 masl), and Mesoamerican race 'Durango' is adapted to the semi-arid highlands of Mexico. Given its mid-to-high altitude origin, bean is sensitive to high temperatures (Porch and Jahn, 2001).

Various authors reported on the effects of high temperature on common bean during and after anthesis, and during day and night hours. In the snap bean cultivar 'Tenderette', all reproductive parameters (pods and seeds per plant; pod length and weight) declined when night temperatures reached 27°C (Konsens *et al*., 1991). These effects were aggravated by day temperatures above 27°C. In a trial with the dry bean cultivar 'Montcalm' under increasing temperatures, but with a constant day/night differentials, Prasad *et al*. (2002) only found an effect on pod set above 37/27°C, although seed set was reduced linearly beginning at 28/18°C onwards. Gross and Kigel (1994) found that a 5-day treatment of 32/27°C at 10 to 12 days prior to anthesis in cultivars PI-271998 and BBL-47 reduced pod and seed set to zero, suggesting that sporogenesis is the most sensitive period. On the other hand, Monterroso and Wien (1990) showed effects on flower and pod abscission with treatments of 35°C day temperatures and 20°C night temperatures. Based on the implementation of different levels of stress in different genotypes at different growth stages, these studies suggest that high temperature can be detrimental at any stage in the days pre- and post anthesis. An estimate of the potential impact of improving common bean for heat tolerance suggested that it could benefit 7.2 million ha (some of which would also benefit by drought tolerance) and this could also expand the highly suitable areas for growth by 54% (Beebe *et al*., 2011). Bean-producing regions that will be subject to increasing heat stress in the short term are lowland central America, central Brazil, northern Uganda, and southern D. R. Congo (Beebe *et al*., 2013b).

c. Soil constraints. Low phosphorus (P) availability: P availability is a limiting factor to bean productivity, especially in tropical soils (Lynch and Beebe, 1995). Root architecture has a great influence on the ability of bean plants to acquire P from the soil (Liao *et al*., 2001; Lynch, 2011). The Peruvian landrace 'Chaucha Chuga' was identified as relatively efficient in acquiring P from low P soils (Lynch and Beebe, 1995). QTL were identified in 'Chaucha Chuga' for a range of root traits that contribute to enhanced P uptake: total root length (Beebe *et al*., 2006), root hair density and organic acid production (Yan *et al*., 2004), and root orientation in relation to soil depth (Liao *et al*., 2004). In addition to P acquisition, differences in P use efficiency (PUE) have been reported among breeding lines (Beebe *et al*., 2013a). The underlying mechanism for this trait remains unknown although PUE appears to be related to an enhanced capacity for remobilization of photosynthates. Some drought resistant lines with improved remobilization expressed superior yield under P limited conditions (Beebe *et al*., 2008; Beebe *et al*., 2013b). Recently, a comparative study using two common bean genotypes with contrasting response to P deficiency (P-tolerant BAT 477 and P-sensitive DOR 364) indicated variations in the microRNA 399-mediated *PvPHO2* regulation within the PvPHR1 transcription factor-signaling pathway (Ramírez *et al*., 2013). Results showed that higher *PvPHO2*, resulting from less efficient PvmiR399-mediated mRNA degradation, in DOR 364 would result in increased *PvPHO2*-mediated degradation of P-responsive proteins, such as P transporter PHT1, which would cause a decrease in P content and P use efficiency in P-sensitive DOR 364.

Aluminum (Al) toxicity: Al toxicity affects as much as 40% of the global bean production, especially in the tropics (Thung and Rao, 1999). In Africa, an estimated 23% of the bean areas are affected by toxic levels of Al (Wortmann *et al*., 1998). The primary effect of Al toxicity is to inhibit root elongation, and thus crops suffering from Al toxicity are assumed to be at greater risk of drought due to limited root development (Yang *et al.*, 2013). Differences in growth of bean plants in Al-toxic soil were previously noted (Foy, 1988). The *P. coccineus* accession G 35346 had excellent vigor in an acid soil in the field and superior root elongation in Al-toxic soil and hydroponic systems in the greenhouse (Butare *et al.*, 2011), and was utilized in crosses to the drought resistant common bean SER 16. The derived line 'ALB 91' expressed much of the root vigor of the tolerant parent and has been used extensively in crosses (Butare *et al.*, 2012).

Mechanisms of Al resistance in common bean were defined using the Al resistant genotype 'ICA Quimbaya' and the Al sensitive VAX-1 (see review by Yang *et al.*, 2013). It was shown that the induced and sustained Al resistance of 'Quimbaya' is mediated by reducing the stable-bound Al in the apoplast thus allowing cell elongation and division to resume. Resistance to Al in common bean is attributed to the release of citrate by the root apex which is mediated by the multidrug and toxin extrusion (MATE) citrate transporter gene. Al resistance was mainly dependent on the capacity to sustain citrate synthesis, thereby maintaining the cytosolic citrate pool that enables exudation. The initial Al-induced inhibition of root elongation in both Al-resistant and Al-sensitive genotypes was correlated with the expression of the 1-aminocyclopropane-1-carboxylic acid oxidase gene (Yang *et al.*, 2013).

Nitrogen deficiency: P. vulgaris is considered, in general terms, to be a poor nitrogen fixer, although field experiments report as much as 100 kg ha^{-1} fixed N in favorable conditions (Hardarson *et al.*, 1993). Common beans with a climbing growth habit consistently fix N (Graham and Rosas, 1977), and can contribute to improved maize yields in crop association (Pineda *et al.*, 1993) or in a crop rotation scheme with maize (CIALCA, 2007). However, SNF in common bean is very sensitive to stress due to drought, low available soil P (Sinclair and Vadez, 2002), or high temperatures. A drought resistant breeding line ('BAT 477') with a bush growth habit maintained a relatively higher level of SNF under drought stress in field trials in Mexico (Castellanos *et al.*, 1996) and in field and greenhouse trials in South Africa (Amsala Fenta, 2012), possibly due to a more vigorous root system that avoided drought and alleviated stress on SNF. A wider selection of drought resistant lines maintained a higher level of acetylene reduction in a greenhouse soil drying experiment (Devi *et al.*, 2013). The same lines also fixed more N in the well watered treatment, suggesting that selection for drought resistance had contributed to SNF capacity.

2. *Genomics and multiple stress tolerance*

Interactions of a particular stress with other factors in the environment, especially other stresses, complicate the selection for stress tolerance (Beebe *et al.*, 2013a; Yang *et al.*, 2013). Drought stress can interact with higher temperatures, or with poor soil fertility that limits root development. Identifying the critical interactions and incorporating these into a selection program is perhaps the most challenging aspect of improving adaptation to abiotic stress factors. Most bean improvement efforts for abiotic stress have been focused on individual stresses, but a few studies considered the effects of multiple stress conditions. Butare *et al.* (2011) found that roots of *P. coccineus* accession G35346-3Q developed better than those of common bean under a combined stress of acid soil toxicity and drought. A few interspecific progenies expressed tolerance to combined stress. For example, the breeding line 'ALB 91' had 12%, 71% and 20% higher yield in Al stress, drought stress and irrigated treatments, respectively, compared to the commercial check. Shallow root development in common bean favors P acquisition, while deeper root development is preferable for accessing moisture and improving drought resistance (Ho *et al.*, 2005; Henry *et al.*, 2010). Yang *et al.* (2010) characterized the combined effects of Al toxicity and drought stress on root growth, with emphasis on the root apex of common bean. Using polyethylene glycol (PEG) to create osmotic stress (OS) and to simulate drought stress, they found that OS enhances Al resistance by inhibiting Al accumulation in the root apices of the Al-sensitive genotype (VAX-1). This effect was related to the alteration of cell wall porosity caused by PEG-induced dehydration of the root apoplast. Physiological and molecular analysis of this phenomenon indicated that genes related to cell wall assembly and modification (*XTHs, BEG, HRGP*) play important roles in the PEG-induced decrease in cell wall porosity (Yang *et al.*, 2011). Studies on short-term effects of Al toxicity and drought stress on root growth in acid, Al-toxic soil showed that drought alleviates Al injury, but Al renders the root apex more drought-sensitive, particularly by impacting the gene regulatory network involved in ABA signal transduction and cross-talk with other phytohormones that are necessary for maintaining root growth under drought stress (Yang *et al.*, 2012).

3. *Strategies for breeding the ideal phenotype*

The phenotype of an organism is fundamentally a manifestation of the genotype's interaction with the environment. An ideotype is a plant with an ideal phenotype that combines the desirable traits and mechanisms to enable its adaptation to a target environment. An integrated improvement of resistance to abiotic stresses is likely to be more productive than considering stresses in isolation (Yang *et al.*, 2013). This raises the question of whether a common ideotype might respond to several constraints simultaneously. We suggest that a common bean ideotype for most bean growing areas (with no risks of terminal drought) with multiple stress resistance would have an extended vegetative period to favor water and nutrient acquisition and accumulation of leaf area and biomass, followed by vigorous remobilization of photosynthates to grain for better harvest index. The aim is to optimize the balance between internal use of carbon resources for structural development, and the benefits gained from such investments in terms of fraction of photosynthates that are translocated to economically important products. By definition this should lead to better yield, and is useful only if it leads us to focus on the factors that maximize each of the two multipliers of biomass and HI.

Soil fertility and Al toxicity in particular limit biomass accumulation. Based on a modeling exercise, Nord *et al.* (2011) concluded that P acquisition would be favored by a longer growth cycle. Time translates into more resource acquisition, which is to say, more P, potassium, calcium, and other nutrients. The rate of root elongation in common bean is drastically reduced in the presence of Al toxicity (Butare *et al.*, 2011; Yang *et al.*, 2013). Slower root growth would likewise be compensated by a longer vegetative phase. In the case of SNF, greater fixation is associated with genotypes with a longer growth cycle, such as is the case of the climbing beans that may mature in 100 to 250 days (Graham and Rosas, 1977; Manrique *et al.*, 1993), compared to bush beans that typically have a cycle of 70 to 90 days. A longer vegetative cycle may result in more carbon for SNF.

On the flip side, a longer vegetative cycle also exposes the crop to risk of drought for a longer time, and augments the expenditure of water from the soil, running the risk of exhausting this resource before the critical grain filling stage. Stomatal control and higher values of TE can ameliorate this risk (Sinclair, 2012), and bean has shown variability for this trait (Devi *et al.*, 2013). To take advantage of greater biomass production under drought, maintaining HI through enhanced remobilization of photosynthate is critical (Ramirez-Vallejo *et al.*, 1998; Assefa *et al.*, 2013; Habibi, 2013; Rao *et al.*, 2013). This trait is of wide value not only in the presence of water deficit (Beebe *et al.*, 2013c), but also to address any potential P deficiency and Al toxicity (Beebe *et al.*, 2008; Beebe, 2012; Beebe *et al.*, 2013a, b). The Colombian landrace 'G21212' has showed excellent photosynthate remobilization capacity under both drought stress and low P availability, and others found that G21212 was also superior under soil compaction (Smith, 2004). Thus, enhanced remobilization and HI represent a generalized tolerance mechanism for major abiotic stresses. Recently, the ′SWEET′ sugar transporters were identified; these are plasma membrane proteins located in the phloem parenchyma, a cell type inside the veins that exports sucrose to SUT1 sugar loaders (Chen *et al.*, 2012). Since the photosynthate mobilization to grain and relative distribution of carbon between vegetative and reproductive growth for optimizing sink capacity critically determine crop yield, further research work is needed to define the role of these SWEET proteins in improving multiple stress tolerance. Functional genomics may contribute significantly to understanding key steps that serve to maintain translocation under stress.

Regarding resource acquisition from the soil, at least two overall root architecture traits appear to be valuable. Longer root hairs would augment the absorptive surface of roots and have almost no energetic cost (Yan *et al.*, 2004; Miguel, 2004). A second trait with wide utility could be greater specific root length, although this strategy might have limitations in compacted or heavy textured soils if roots with a smaller diameter have a diminished ability to penetrate the soil (Butare *et al.*, 2012).

Finally, if the crop cycle terminates with a rapid and synchronized maturity and "dry down" of the crop, this bean ideotype will be more acceptable to farmers. This will avoid a crop cycle that is excessively long, or a crop that reverts to vegetative growth under late season rainfall – a situation that complicates harvest or results in green leaves that stain the grain with chlorophyll during threshing.

If such a productive ideotype can be established, other stress-specific traits can be built around this model. While apparently a very simple model, maximizing remobilization is contrary to the underlying evolutionary tendencies of a bean crop that is vegetatively vigorous. We have referred to the wild bean model whereby extreme vegetative vigor is accompanied by low HI. In other words, in the balance between vegetative growth and reproductive development, partitioning may be tipped one way or the other, and it is not easy to optimize both in well synchronized succession that would augment yield. The search for an unambiguous shift to reproductive development under different climatic and edaphic conditions is a key to complement strategies that lead to greater biomass, either genetically or through agronomic management. Continuing selection under drought stress has revealed breeding lines with superior capacity for nutrient remobilization (Beebe *et al.*, 2008). Another strategy to enhance sink strength is to introgress genes to common bean from *P. acutifolius* (Rao *et al.*, 2013). Results in this regard are promising. One or the other of these strategies could assure grain fill even under drought stress, while permitting progress in tolerance or resistance to other types of abiotic stress.

B. Chickpea

Being grown under rainfed conditions in most production regions (90%, Kumar and Abbo, 2001) drought is by far the major abiotic stress for chickpea in cultivation during the post-rainy season in Asia. There the crop is fully grown under residual moisture and is bound to face water limitation at some point during its cropping cycle, usually around and after flowering. Drought also affects chickpea Mediterranean type production environments where the crops depend on incoming rainfall during the season, but finish its cycle without rain and also faces terminal stress. Heat stress is now becoming an important constraint for chickpea production in India, where the production area (about 6 M ha), i.e., about two third of the world area, has largely shifted from North to South. Therefore it is now cultivated mostly under short cropping seasons where flowering meets with the first heat waves of the summer during flowering (Gaur *et al.*, 2010). Over the last few decades, chickpea planting area has been reduced in favor of wheat production, and therefore pushed to more marginal areas where soil salinity is also a problem. In conclusion and by order of importance, drought, heat and salinity are the main three abiotic stresses that limit chickpea productions.

1. Abiotic stress responses

a. Drought. Terminal drought, i.e., a water deficit occurring around and after anthesis is the main type of drought that chickpea faces, both in tropical and temperate environments.

The first strategy used by breeders to cope with terminal stress has been to develop shorter duration varieties in which duration matches water supply (Summerfield *et al.*, 1990; Berger *et al.*, 2011), and quantitative trait loci (QTL) for flowering time have been identified (Kumar and van Rheenen, 2000). In India, it was stated that the different latitudes of production needed cultivars having different phenological characteristics, namely longer duration in northern latitudes and shorter durations in the South (Berger *et al.*, 2006). This has shaped the phenological characteristics of cultivars that breeding programs have developed across India in the last few decades. The rationale is that northern environments have cooler temperatures during the February–March season allowing longer grain filling period while the season is shorter in the South and requires early flowering to escape heat. These views have been challenged recently: in India there would actually be no need for any particular phenological requirements and that an intermediate duration type with about 820 thermal unit to reach flowering and about 660 thermal units for the grain filling period would allow the highest possible yields across a range of latitudes from about 13 to 32 °N (Vadez *et al.*, 2013a). These modeling results in fact agree with experimental results from Berger *et al.* (2011).

Much of the work on drought in the last three decades (Saxena, 1984) or so have focused on developing chickpea cultivars with deeper and more profuse root systems to tap more water from the soil profile. Some positive relationships have been identified between rooting depth and density and seed yield (Kashiwagi *et al.*, 2005). However, in that study the relationship held only under the harsher stress conditions and not under milder stress, and using a 257 recombinant inbred line (RIL) population developed between two parents contrasting for root traits, no relationship was found between the root traits and seed yield (Serraj *et al.*, 2004). The difficulty to sample and assess root systems in the field has led to the development of cylinder-based cultivation to assess root growth, and this method has allowed revealing a very large range of variation for root traits in the mini-core collection of chickpea (Kashiwagi *et al.*, 2006). The contrasting germplasm from that study has been taken further by the breeding to develop cultivars with improved root systems (Gaur *et al.*, 2008). Using populations developed earlier, a QTL on linkage group 5 for root trait has been identified, explaining about 30% of the phenotypic variation (Chandra *et al.*, 2004). A number of QTL hot spots has more recently been identified using several RIL populations, including one on linkage group 5 where the QTL for root traits was initially discovered (Varshney *et al.*, under review). SuperSAGE, an improved version of the serial analysis of gene expression (SAGE) technique, has also been employed to analyse transcriptome changes induced by drought in chickpea roots (Molina *et al.*, 2008). This comprehensive study demonstrated that signal transduction, transcription regulation, osmolyte accumulation, and ROS scavenging undergo a strong transcriptional remodeling in chickpea roots in early drought stress responses, suggesting potential targets for breeding for drought tolerance.

More recently, chickpea genotypes contrasting for their seed yield under terminal drought conditions have been identified (Krishnamurthy *et al.*, 2010). Some of these have been used to investigate traits, other than root, that could also contribute to terminal drought adaptation. Water conservation traits (low leaf conductance at vegetative stage, smaller leaf canopy, higher soil moisture thresholds for the transpiration decline) have been identified as common traits among germplasm achieving the highest yield under terminal stress (Zaman-Allah *et al.*, 2011a). The rationale behind these traits is that conserving water at vegetative stage would make more water available for the reproduction and grain filling period. Indeed, a recent study carried out in a lysimetric system (Zaman-Allah *et al.*, 2011b) has shown that higher yielding genotypes were those extracting less water during the vegetative stage, in the absence of any stress, and those extracting more water during reproduction and pod filling. The total water extracted from the soil profile varied between genotypes, but did not distinguish the 8 sensitive genotypes from the 12 tolerant lines tested (Zaman-Allah *et al.*, 2011b). These data offer new insight on drought tolerance research in chickpea and demonstrate that coping with terminal water stress also depends on water conservation traits. Similar strategy has been characterized in other crops facing terminal stress like cowpea (Belko *et al.*, 2012) or pearl millet (Vadez *et al.*, 2013b). These traits may be antagonistic to the root trait QTL reported above, which reflect a higher speed of rooting. Indeed, the root trait QTL identified earlier co-maps with a shoot QTL explaining more than 50% of the phenotypic variation (Chandra *et al.*, 2004) that might represent a vigor QTL. Higher early vigor would lead to fast soil water depletion and therefore the water saving traits may work in opposition to the fast rooting. Two modeling studies in soybean and chickpea are showing exactly this, i.e., a faster root growth would lead to yield decrease in most environments (Sinclair *et al.*, 2010; Vadez *et al.*, 2012a), although in chickpea a faster rooting would still have a beneficial effect in the case of short duration cultivars evolving in short duration environments (Vadez *et al.*, 2012a). In fact, increased water extraction at depth by 20 cm would increase yield by about 10%, while a modest irrigation of 30 mm at the beginning of seed growth would increase yield by 30-40% (Vadez *et al.*, 2012a), which gives a perspective on avenues for crop improvement under drought in chickpea.

In summary, while much of research on drought in the past four decades has focused on developing short duration genotypes and on harnessing deeper and more profuse rooting traits, new insights are coming from water conserving traits, which would allow the crop to have water available during critical stages of the crop cycle. However, none of these traits offers a solution to all drought situations and none of these traits should be seen as a one-fits-all. Therefore, future research on drought needs to tackle how plant traits fit to particular stress environments. In this research, crop simulation modeling is a critical tool to guide the choice of breeding targets.

2. *Heat and salinity*

These two abiotic stresses are grouped together because there has been much less research, but also because both seem to be affecting mainly the reproductive biology, as it has been reported earlier in other legumes (Duthion and Pigeaire, 1991). In chickpea, only recently has heat stress been tackled and short exposure to temperature above 35°C decreased pod number (Wang *at al.*, 2006). Sensitivity of male and female reproductive organ is hypothesized as sensitive to heat stress (Nayyar *et al.*, 2005). Chickpea genotypes tolerant to heat stress have been recently identified (Krishnamurthy *et al.*, 2011). Pollen viability and germination was more sensitive than stigma receptivity in chickpea and at a regime of 35°C/20°C day / night temperature, the pollen germination of the tolerant genotype was down to about 40% while that of sensitive genotype was 0% (Devasirvatham *et al.*, 2012).

In relation to salinity, we will refer to a recent exhaustive review written on the topic (Flowers *et al.*, 2009). While much of the early work has been carried out at vegetative stage, looking at plant growth response to salt stress, recent reports have focused on looking at yield response under a controlled saline treatment with homogenous stress application in large pots set up outdoors (Vadez *et al.*, 2007; Krishnamurthy *et al.*, 2011). These studies have revealed that large variation for seed yield under salinity exists. Vadez *et al.* (2007) reported that differences in yield were not related to differences in shoot growth, although shoot growth could still play a role on this (Vadez *et al.*, 2012b). Also, differences in seed yield were not related to differences in Na accumulation in the shoot, which brings a new insight in salinity tolerance research, although sensitive lines had slightly higher Na in the seed for a limited number of genotypes (Turner *et al.*, 2013). In fact, tolerant entries produce simply more flowers and have more tertiary branches than sensitive lines (Vadez *et al.*, 2012c). Differences between tolerant and sensitive lines also seem to relate to the capacity to keep a large number of seeds under salt stress (Vadez *et al.*, 2007), although pollen viability, germination, and growth *in vivo* were not affected by salinity (Turner *et al.*, 2013). Future work on salinity would need to untangle what mechanism of the reproductive biology is affected by salt stress and then whether the salt application has an effect through ion toxicity or osmotic effect.

C. Pea

Pea is a crop cultivated world-wide being consumed as dry pulses mainly for animal feed, or as fresh peas for human consumption (Smýlkal *et al.*, 2012). It is the third pulse crop in importance with over 6 million hectares following soybeans and beans (FAO, 2011). Abiotic stresses caused by adverse environmental conditions are responsible for heavy economic losses on pea crop being drought, high/low temperatures, and salinity the most important abiotic constraints. The extent of the yield losses depend largely on the intensity, duration and distribution of the adverse conditions. For instance, water requirements of pea are relatively high particularly during germination and flowering. Thus, water limitations at flowering lead to a shorter flowering period and abortion of flowers (Ney *et al.*, 1994; Gallegos and Shibata, 1989). As a consequence, pod and seed numbers are reduced decreasing yield dramatically (Andersen and Aremu, 1991). During pod-filling phase, the sensitivity of peas to water stress is lower reducing mainly the number of pod seeds (Mahieu *et al.*, 2009). Flowering is also a crucial stage in which sensitivity to high and low temperatures is particularly accused (Ali *et al.*, 1994).

Development of new pea varieties adapted to a wide range of environmental conditions is the main aim of pea breeding programs (Moneim *et al.*, 1990) being a crucial goal for improving competitiveness. As example, competitiveness could be improved by the development of autumn-sown peas in order to benefit from a higher biomass production, as well as, to avoid drought and heat stresses of late spring. Breeding programs are thus carried out to release winter hardy cultivars, able to survive freezing temperatures and other associated winter stresses. Although selection for winter hardiness has generally been performed through the field observation of winter damages and/or winter survival, which are largely attributable to insufficient freezing tolerance, it would benefit from the knowledge on physiological traits associated to freezing tolerance (Stoddard *et al.*, 2006). Indeed, breeding for tolerance of any of the abiotic stresses above mentioned is a complex phenomenon for which a sound knowledge of the mechanisms leading to abiotic stress tolerance is crucial.

1. *Abiotic stress responses*

Under water and salinity stress the uptake of water and minerals is disturbed and hence photosynthetic activity decreases. Particularly, photosynthesis is well known to be sensitive to heat stress (Berry and Bjorkman, 1980). Reduction of up to 78% in photosynthesis has been described in pea following drought (Moran *et al.*, 1994) reaching up to 80% of reduction when temperature increased to 45 °C (Haldimann and Feller, 2005). According to this, diverse chlorophyll fluorescence parameters have been shown to reflect the ability of pea plants to maintain photosynthesis under chilling (4°C to 10°C) and genetic variability for some of these parameters has been evidenced (Georgieva and Lichtenthaler, 1999, 2006). Reduced photosynthesis, lead to reduction of growth, by mean of fresh and dry weight and leaf area in pea (Magyar-Tabori *et al.*, 2011).

Tolerance responses of pea to abiotic stresses include a series of morphological/physiological features that allow pea plants maintaining photosynthesis. Thus, the level of photoassimilation has been reported as an appropriate screening parameter for salt tolerance in pea genotypes (Shahid *et al.*, 2012). Maintenance of photosynthesis under stress, particularly drought or salinity, implied a delicate equilibrium between the water loss and CO_2 uptake. Thus, morphological changes to increase water access have been reported in pea cultivars in which, resistance to drought was correlated with a smaller root-to-shoot ratio than in sensitive genotypes (Grzesiak *et al.*, 1997). In addition, field peas exposed to water stress had thinner roots that grow deeper into the soil to access water resources (Benjamin and Nielsen, 2006). By contrary, osmotic stress, provoked by PEG 6000 in pea plants, induced a shortening of the primary root and an increase of the lateral root number (Kolbert *et al.*, 2008). In addition, under salinity conditions, roots became constricted above apex, thickening the region over the constriction and curving root tips (Solomon *et al.*, 1986). Semi-leafless pea types are reputed as more tolerant to water deficit than leafed type peas attributing this tolerance to the reduced leaf area of the semi-leafless plants (Gonzalez *et al.*, 2002). However this tolerance was not associated to a lower transpiration of the semi-leafless plants, that was not significantly different from the conventional leafy plants, but to a higher osmolarity of tendrils of the epidermal vacuoles (Gonzalez *et al.*, 2002). Structural changes related with the cuticle have also been described in both drought and salt tolerant pea plants (Poljakoff-Mayber, 1975; Sanchez *et al.*, 2001). Particularly epicuticular waxes, that control the loss of water from the cuticle, increased significantly together with an increase of the residual transpiration rate in peas under drought (Sanchez *et al.*, 2001).

Under most environmental stresses the reduction of photosynthesis is correlated with an increase in photorespiration. However, studies conducted in pea, under a variety of conditions provide partly contradictory data. For example, Fedina *et al.* (1993, 1994) showed an increase in different parameters indicative of high photorespiration such as the CO_2 compensation point or the activity of the glycolate oxidase as consequence of salt stress, whereas other authors showed a reduction of up to 44% in the glycolate oxidase under drought (Moran *et al.*, 1994). This contradiction may be due to the intensity of the stress since, under severe stress, reactions of the Calvin cycle might have been inhibited, which could result in reduced contents of RuBP (Sharkey and Seemann, 1989) and, consequently, in lower rates of RuBP oxygenation.

Linked with the photorespiration and/or as a consequence of the imbalance between the CO_2 and the electrons derived from the light reactions, reactive oxygen species (ROS) are generated in plants subjected to most environmental stresses. Indeed, this imbalance occurs under drought, cold, heat, high light intensity, UV radiation or salinity stress (Shao *et al.*, 2008). In addition, toxic metals not considered as redox-active metals such as nickel has also been reported to stimulate the production of ROS in pea (Gajewska and Sklodowska, 2005). Thus, generation of ROS is an acknowledged feature of peas under most environmental stresses (Moran *et al.*, 1994; Hernandez and Almansa, 2002; Gajewska and Sklodowska, 2005; Noreen and Ashraf, 2009; Panda and Matsumoto, 2010). Excess of ROS may cause peroxidation of membrane lipids leading to a loss of the membrane integrity and hence cell functionality. Tolerance responses linked to the reduction of the damage caused by ROS, may be achieved by reducing the generation of ROS or increasing the antioxidant machinery to scavenge the generated ROS. Indeed, over-expression of antioxidant genes has been shown to confer drought tolerance in pea (Hernandez *et al.*, 2000; Alexieva *et al.*, 2001; Hernandez and Almansa, 2002). In plant cells the enzymatic scavenging system for reactive oxygen intermediates consists of enzymes such as, superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), monodehydroascorbatereductase (MDAR), dehydroascorbatereductase (DHAR), glutathione peroxidase (GPX), and glutathione reductase (GR) included in the so-called water-water cycle (Asada, 2000). Alexieva *et al.* (2001) reported that in pea plants subjected to water stress the specific activities of antioxidant enzymes increased. Interestingly the same authors found a reduction of catalase and SOD activity whereas Moran *et al.* (1994) found a decrease of pea catalase, but an increase of SOD under water stress. These differences may arise from the different tolerance level of the genotypes tested, since an increase of SOD suggests a major photosynthetic imbalance leading to higher ROS generation. Interestingly both authors reported an increase of peroxidase activity leading to a reduction of H_2O_2. In addition, increases of the transcript levels of the ascorbate peroxidase and SOD have been described to parallel the decrease of stomatal conductance in drought-stressed pea plants (Mittler and Zilinskas, 1994). Overall, under salt stress, a rapid increase of SOD followed by increase of ascorbate peroxidase has been related to stress tolerance (Hernandez *et al.*, 2000; Hernandez and Almansa, 2002). However, in a recent study on pea plants subjected to salt stress, the response of tolerant and sensitive cultivars with respect to the generation of enzymatic and non-enzymatic antioxidant metabolites was not consistent and only catalase activity was found to be a reliable marker of salt tolerance (Noreen and Ashraf, 2009). The low consistency in the results might be due to the different level of stress experimented by the plants since induced tolerance mechanisms are engaged after a determinate threshold. A high induction of a determinate stress associated metabolite/enzyme may indeed indicate that the plant is suffering the damages associated to this stress. Hence, it is important to distinguish between the responses engaged to alleviate advanced damages from those avoiding the damage in the plant which can be considerate as more effective tolerance response (Sanchez *et al.*, 2011). Induction of ROS and antioxidant enzymes of the water-water cycle has been also reported in pea plants following exposure to heavy metals such as aluminum, nickel or cadmium (Gajewska and Sklodowska, 2005; Rodriguez-Serrano *et al.*, 2009; Panda and Matsumoto, 2010) highlighting the importance of the antioxidant machinery to cope with environmental stresses.

In addition to the energy consumption by photorespiration, and the dissipation of energy by electron transport to O_2 by antioxidant enzymes/metabolites of the water-water cycle (Asada, 2000), non-photochemical quenching linked to the formation of zeaxanthin in the xanthophyll cycle and an increased proton gradient across the thylakoid membrane have been reported to contribute in pea to drought tolerance (Iturbe-Ormaetxe *et al.*, 1998).

Linked with oxidative damage, but not only related to it, accumulation of osmotically active metabolites such as amino acids, glycine betaine, sugars, or sugar alcohols are known to occurr in the cytoplasm contributing to high turgor and to protein and membrane stabilization, alleviating stress associated damages in pea (Sanchez *et al.*, 1998; Shahid *et al.*, 2012). Thus, drought tolerant pea genotypes have been reported to have better turgor maintenance by accumulation of soluble sugars and proline. Although all plants subjected to water stress increased the sugar content proportionally to osmotic adjustment, sugar accumulation was higher in the most resistant genotypes (Sanchez *et al.*, 1998). Significant increases of proline, valine, myo-inositol, GABA, threonine, homoserine and trigonelline have also been detected in a metabolomic analysis of pea plants subjected to drought stress (Charlton *et al.*, 2008). In addition, accumulation of soluble sugars in the leaves during the low temperature treatment preceding frost in a controlled conditions experiment has also been reported (Bourion *et al.*, 2003). Similarly, under salt stress, Shahid *et al.* (2012) showed that pea tolerance was due to a higher osmolyte accumulation in their tissues. However, field experiments with pea genotypes had not always found a significant correlation between osmotic adjustment and yield performance, highlighting the complexity of the improvement of yield under drought (Khan *et al.*, 1996).

Beyond the redox and osmotic properties of several of above mentioned metabolites, some of them such as $H_2O_{2,}$ sugars or polyamines, act as signal molecules that may impact ABA, auxin and ethylene signaling (Hanson and Smeekens, 2009). Signaling is particularly important during the abiotic stress responses due to the complexity of metabolic pathways and processes engaged during the tolerance responses. Whereas most of knowledge on signaling during abiotic stress responses has been developed on model plants (Xiong *et al.*, 2002), recent advances on the functions of the signaling molecule nitric oxide (NO) during abiotic stress have been attained in pea (Corpas *et al.*, 2008; Rodriguez-Serrano *et al.*, 2009; Ortega-Galisteo *et al.*, 2012). These showed that most abiotic stresses including low and high temperature, continue light and high intensity induced increases of NO and *S*-nitrosothiols together with an increase in the proportion of *S*-nitrosylated proteins (Corpas *et al.*, 2008). In addition, during cadmium stress in pea, six peroxisomal proteins were identified as putative target of *S*-nitrosylation involved in photorespiration, β-oxidation and reactive oxygen species detoxification. Interestingly, the activity of three of these proteins, catalase, malate deshydrogenase and glycolate oxidase was inhibited by NO donors (Ortega-Galisteo *et al.*, 2012).

2. *Breeding approaches*

Although efforts have been made to apply molecular approaches for breeding pea under abiotic stress, there is no comparison with what have been done for disease improvement. Thus, 76 QTLs have been described so far in pea for 11 traits, but none of them with the exception of the recently reported freeze tolerance QTLs, were related to abiotic stress (Dita *et al.*, 2006; Mc Phee, 2007). Using the Pop2 RIL population, derived from a cross between the freezing tolerant line Champagne and the sensitive line Terese, Lejeune-Hénaut *et al.* (2008) and Dumont *et al.* (2009) repeatedly detected four main QTL regions for frost tolerance in field or controlled conditions. Coinciding with two of these regions, QTL for physiological traits assumed to be associated with freezing tolerance, were also reported. Such were QTL for glucose and raffinose content in the leaves and for the activity of RuBisCO. Candidate genes underlying freeze tolerance QTL in pea have sometimes been identified. It is the case for the flowering *Hr* locus colocalizing with the most explanatory freezing tolerance QTL in Pop2, which is suspected to influence winter frost tolerance by delaying floral initiation until after the main winter freezing periods have passed (Lejeune-Hénaut *et al.*, 2008). *Hr* has been shown to be an ortholog of *EARLY FLOWERING 3* (*ELF3*) known to be involved in circadian clock function (Weller *et al.*, 2012). Other positional candidate genes related to freezing tolerance mechanisms were proposed by Legrand *et al.* (2013) following mapping of genes differentially expressed between Champagne and Terese under cold exposure.

Proteomic and transcriptomic approaches, combined to physiological measurements, have also been carried out in pea. Taylor *et al.* (2005) compared the effects of different abiotic stresses, i.e., drought, chilling, and herbicide, on the mitochondrial proteome of pea and tackled quantitative differences in more than 30 proteins. Proteins commonly induced under the different stresses were observed. In particular, the degradation of glycine decarboxylase and serine hydroxymethyltransferase was provoked by the three treatments, although with quantitative differences. Interestingly, the treatments induced also very different responses for various classes of HSPs: a HSP90 was found to be induced by drought and chilling but not by the herbicide; a HSP70 decreased in response to the herbicide only; HSP22 was induced by all three treatments. In addition recent work explored the protein responses to cold within the pea species (Dumont *et al.*, 2011; Grimaud *et al.*, 2013). In order to discriminate chilling from freezing tolerance responses, the freezing tolerant line Champagne and the freezing sensitive line Terese were compared under low temperature and control treatments. Grimaud *et al.* (2013) showed that cold exposure induces higher aerial biomass production, while freezing tolerance is more related to early higher number of chloroplasts and higher amounts of chlorophylls. The capability of Champagne to develop freezing tolerance is also linked to an early ability to maintain optimal energy production, which is achieved by preventing photo-inhibition through optimization of the photosystems stoichiometry, capability to start additional pathways such as cyclic electron transport around PSI and to induce dynamic changes in carbohydrate and protein synthesis and/or turnover, which support the previous physiological work above stated. At the transcriptomic level, Lucau-Danila *et al.* (2012) also pointed out that Champagne showed a better capability to adjust its photosynthetic apparatus to resist photoinhibition in comparison to Terese. Higher concentrations of raffinose in Champagne also observed in this study could be in compliance with a stabilizing action of this molecule on PS II. Besides, genes related to the response to oxidative stress, stabilization of proteins or RNA secondary structures, hormone metabolism or cell wall composition were also found to be up-regulated in Champagne. Most of the freezing tolerance mechanisms suggested at the transcriptomic level were also revealed by the proteomic study of Dumont *et al.* (2011).

3. *Future perspectives*

Efforts have been made to produce pea stress tolerant genotypes based on the knowledge of the plant response to stress and the mechanisms involved described above but improvement by traditional breeding methods are limited by the complexity and multigenic nature of the tolerance responses. For some traits like recently frost tolerance, QTL mapping is however paving the way toward marker assisted selection. Despite the complexity of most abiotic stresses, stress tolerant cultivars have been bred in several occasions introducing traits from stress-adopted wild relatives or landraces (Bartels and Sunkar, 2005). Particularly landraces have considerable potential to improving abiotic stress tolerance since the transfer of beneficial traits from them is relatively straight-forward in that there is no barrier to crossing. For instance, a deep rooting landrace well adapted to a high range of temperatures from Ethiopia has been reported (JI1432). In addition, *P. fulvum* is a possible source of stress tolerance for cultivated pea, particularly for drought, since, its main root penetrate to greater depths at a rapid rate in the soil (Ali *et al.*, 1994). Accessions of *P. elatius* adapted to frozen temperatures have also been reported (Ali *et al.*, 1994). In addition, since genetically modified pea has a relatively low risk for the environment (outcrossing level $<1\%$), gene transformation could arise as an useful tool for pea breeding (Mc Phee, 2008). However, up to date very few gene transformation work were carried out for improving pea for abiotic stress tolerance may be due to the complexity of the plant tolerance mechanisms above presented (Grant and Cooper 2003; Jewell *et al.*, 2010). Interestingly, several genes related to osmolyte production in pea were recently cloned, and the mannitol phosphate dehydrogenase (*mt1D*) introduced in the pea genotype "Akt" for improving its drought tolerance, albeit the conclusion on the tolerance of the regenerants was not delivered yet (Molnár, 2008).

D. Faba Bean

Up to today, faba bean improvement of adaptation to abiotic stresses was mainly achieved indirectly via breeding for grain yield. In spite of such progress, a main common characteristic of the species – beneath its basic tolerance to slightly saline soil (Katerji *et al.*, 2011) and to mild frost – is its preference of cool, moist conditions, such as spring and summer in England or winters and spring of the Mediterranean Basin. Faba bean is sensitive to drought stress, whether occurring as intermittent or terminal water deficit (e.g., McDonald and Paulsen, 1997).

To uncover, understand and exploit genetic variation for stress tolerance, the stress needs to be specified. As an example, level and pattern of applied drought stress varies widely among researchers (e.g., Grzesiak *et al.*, 1997; Nerkar *et al.*, 1981). Under water stress, the plant may find virtually unlimited amount of water yet hard to take up or a limited offer of water as in terminal drought. With intermittent stress, plants are allowed to recover. Nevertheless, genetic differences for recovery have been barely analysed so far (Khan *et al.*, 2010). Drought stress may or may not be separated from heat stress, from low air humidity and from further intervening features (Amede *et al.*, 1999; Link *et al.*, 1999).

1. *Abiotic stress responses*

a. Drought. In general, promising traits to be analyzed for drought tolerance are shoot and root morphology and developmental pattern, small-scale anatomy such as stomata features, physiological traits belonging to osmotic adjustment or to water-use efficiency and related items.

In temperate and semi-arid climate, fast development is generally decreasing drought penalty. In Germany, spring faba bean need about 12 days from sowing to first photosynthesis, whereas e.g., spring pea needs only 7 days, mainly because faba beans are sown deeper, need a higher temperature sum (5700°C > 3300°C) than pea and more water per seed (about 3.8g > 1.5g) to germinate (Schmidtke, 2012). Smaller-seeded crops and weeds realize, compared to faba bean, a head start. Water that is transpired by weed or lost by evaporation because ground cover is not yet realized increases threat of future drought. On the other hand, speedy canopy closure to minimize evaporation may be a minor topic for autumn-sown beans. Autumn-sowing reduces the drought-threat-driven haste; ground cover will anyway occur only after winter and much earlier than with spring sowing; and larger seeds produce more vigorous, larger-leaved juvenile plants. This may speak in favor of winter faba beans being larger-seeded than spring faba beans.

The genetic diversity of reactions to temperature and day length does seemingly not limit a timely approach of locally adapted faba beans to flowering in the many established growing regions (e.g., China, Ethiopia, Nile Valley, Mediterranean Basin, Central, West and North Europe, Andean South America).

The peculiar reproductive mode of faba bean is a further moment of loss of time, thus of increased risk to suffer from drought. *Vicia faba* is partly cross-fertilized by honey bees and bumble bees. Its roughly 40% to 50% of outcrossing is highly depending on genotype, inbreeding status and actual environment (Palmer *et al.*, 2009). Drought considerably reduced autofertiliy, thus reducing options to escape by speedy development (Stoddard, 1986).

Prospects of monogenetic, altered morphology such as terminal inflorescence types, stable types (stiff-straw) and of independent vascular supply types for dry environments are raising little optimism (Frauen and Sass, 1989; Sass and Stelling, 1989; Patrick and Stoddard, 2010). No stiff-straw cultivars (Boss, Mythos) are on the market any more, in spite of this type causing shorter, thinner stem and smaller leaflets, candidate features of a drought-tolerant ideotype. The 'terminal inflorescence' type may promise escape because of earlier maturity, yet is barely discussed in relation to drought escape. The so-called 'independent vascular supply,' coined by Gates *et al.* (1983) to reduce intra-raceme competition between pods was "quietly dropped" (Link, 2009; Patrick and Stoddard, 2010).

Müller and Ehlers (1986) compared spring faba bean cv. Diana with spring oats cv. Leanda for root and stomata features across two years in field trials. The majority of roots faba bean were found within 1m soil depth, whereas oats has roots up to 1.5 m deep. These findings support that oats could extract more water from soil. Moreover, faba bean showed stomata conductance of below 4 g $H_2O/(m^2s)$, compared to about 8 g $H_2O/(m^2s)$ of oats. Thus, faba bean is characterized by an early, very sensitive stomata closure, avoiding marked water loss. Such behavior reduces the faba beans yield capacity. Breeders should pre-pone faba bean's maximum development by about two weeks – this is promised by winter faba beans. Moreover, root length and depth should be genetically increased and mutual shading of the faba bean canopy could be decreased by breeding.

For nitrogenase activity, faba bean was found to be most drought-susceptible at flowering time (Plies-Balzer *et al.*, 1995). Yet, nitrogen concentration in stressed plants was never reduced compared to control, thus seemingly nitrogen fixation under drought is not a major yield-limiting factor. In pulses, we see this general discussion of competition between vegetative sink versus reproductive sinks. A mild water shortage during flowering is favorable, since it limits vegetative growth allowing a yield and harvest index as high as in non water limiting conditions (Grashoff, 1990).

Karamanos (1978) concludes from field studies that mild stress moreover may cause a gradual hardening of a faba bean crop, shown by a lessened response to future drought in leaf number and leaf area than if non-hardened. A previous stress can, as shown by Davies (1978), dramatically decrease the sensitivity of stomata for an actual stress. Thus, hardening to drought must be a feature that improves the water status under drought.

Amede *et al.* (1999) and Link *et al.* (1999) agreed in the correlation between low plant height and high drought tolerance, thus breeders may select for the higher heritable plant height pattern as a proxy for yield reactions. A simple ideotype under drougth could be a xeromorphic type, with thick small leaves, thick cuticula, few, small stomata. Yet, Nerkar *et al.* (1981) found that a tall, large-leaved type such as Wierboon with high transpiration per leaf area and high water use efficiency would be characterized as drought-tolerant. Wierboon had high growth rate, high net assimilation rate, and the authors conclude from their data that selection for superior water use efficiency could well be conducted under adequate irrigation as well as under stress condition.

Khazaei *et al.* (2011, 2013a, b) applied the FIGS (Focused identification of Germplasm Strategy) concept to two very large samples of faba beans ($N = 200$ each), with provenance from dry and wet agro-ecological environments. The authors try to learn from such differential adaptation how this may have altered drought-related features of the faba bean. Under non-stress conditions, the traits identified to be most important for drought adaptation were leaflet and canopy temperature and relative water content, with marked temperature depression and high water content being associated with the dry-provenance faba beans; the dry set of faba beans had the higher mean transpiration rate and thus cooler leaves than the wet set (assessed without stress). Leaf temperature depression was negatively and significantly correlated to stomata conductance and transpiration rate ($0.59 < r < 0.85$) and positively correlated with intrinsic water use efficiency ($r = 0.75$ in the dry set and $r = 0.51$ in the wet set) under non-stress conditions. Looking on stomata frequency and stomata length, the dry set of faba beans had less frequent and larger stomata (assessed without stress) than what the wet set of faba beans showed. Less and larger stomata may be the genetic adaptation to drought. Looking on the effect of experimental drought stress on these faba beans, Khazaei *et al.* (2013a, b) reported an increase of stomata density and a decrease of their size, accompanied with the expected decrease in gas exchange. Increase of stomata density may partly be caused by drought-induced decrease of leaflet size. Finally these authors concluded that, for faba beans, there is no support of reduced stomata frequency and size being favorable under drought. The well-known drought tolerance inbred line ILB938/2 (Abdelmula *et al.*, 1999; Khan *et al.*, 2007) had, as example, a rather high stomata density. Stomata frequency and stomata size showed a clear negative, genetic correlation, counterbalancing each other presumed effects on drought tolerance. Hence, stomata opening and closing behavior and features such as root traits and cuticula traits must have marked impact on the drought tolerance of faba bean. Whether adaptation to drought causes a general increase or decrease of stomata frequency and size seem to not yet be fully resolved.

Opinions are divided as to osmotic adjustment (Serraj and Sinclair, 2002). Amede *et al.* (1999), based on greenhouse experiments, explained the clear genetic differences between solute accumulation mainly by differential accumulation due to differential water loss and not by active solute synthesis. The authors conclude that there was not true osmotic adjustment in this material. Similar to Amede *et al.* (1999), Katerji *et al.* (2002) found that the cv. Superaquadulce did not respond with osmotic adjustment to moisture stress. Balko (2005) agrees on a low ability of faba bean to osmotic adaptation. Yet, high proline accumulation was going along with low yield depression due to stress. Khan *et al.* (2010) doubt whether faba bean can actively adjust turgor and osmotic potential as response to drought.

Beneath proline, further compounds are discussed. El-Tayeb (2006a, b) compared Giza 40 with Giza 667. Giza 40 is a drought tolerant cultivar, whereas Giza 667 is drought susceptible

(Soliman *et al.*, 2011). He compared the performance of potted juvenile plants at 90% and 40% field capacity. Drought stress caused a larger increase in lipid peroxidation (measured via malondialdehyde, a breakdown product of multiply desaturated fatty acids). A low level of 0.6 malondialdehyde per g fresh weight of both cultivars increased due to drought to 2.7 (tolerant cv.) and 5.4 (susceptible cv.). Similarly, he reports a greater level and drought-induced increase in catalase and peroxidase activity in the susceptible cv. than for Giza 40.

Assessment of the discrimination against the heavier carbon isotope, delta ^{13}C, is meanwhile a standard approach to indirectly measure stomata conductance and water use efficiency (Condon *et al*., 2006; Khan *et al.*, 2010), including in faba bean (Khan *et al.*, 2007). The importance of ^{13}C discrimination is generally accepted, yet, selection direction seems unclear; e.g., Balko *et al.* (2013) found delta ^{13}C to be positively correlated to grain yield under drought stress (terminal drought) yet negatively so under non-stress conditions. Khan *et al.* (2010) take delta ^{13}C as the 'gold standard' of physiological drought tolerance assessment. Yet, it is rather costly compared to e.g., assessing leaf temperature depression with infrared thermometer or infrared camera (Costa *et al.*, 2013). Indeed, leaf temperature depression as a direct result of transpiration is promising to reflect water use efficiency and stomata conductance in faba bean (Khan *et al*., 2007). Temperature differences are mainly meaningful under non-stress conditions, but under stress, with presumably all stomata closed, differences are insignificant, depending on the severity of the stress applied. Given the lack of markedly drought-tolerant faba bean accession, alien genes should be introgressed from other crops. Alas, faba bean cannot yet be crossed with any of its related species such as *V. peregrina*; thus, genetic transformation is a tempting tool to acquire additional diversity. Hanafy *et al.* (2013) report their recent success in transforming faba bean (tannin-free cultivar Tattoo) with the PR10a gene from potato. This transgene was taken because of its impact on salt or drought tolerance in potato. Fertile transgenic faba bean plants showed clear and convincing effects, promising a novel approach to improve drought and salt tolerance.

Environmentally-caused phenotypic modification (acclimation) as response to stress may differ in direction and size from genetic adaptation. Heterosis-caused genetic change, giving tolerance, may well differ in direction and size from a non-heterotic genetic adaptation. This is true even in spite of the very tempting gain especially under stress: Abdelmula *et al.* (1999) reported from 27 F1 hybrids along with their parents in rain-out shelters in four environments, with mid-parent heterosis (grain yield) of 52% under stress conditions and 39% without stress. More recently, Flores *et al.* (2012, 2013) reported high GxE interaction in faba bean adaptation to both autumn and spring sowing under European conditions, supporting specific breeding for each of the three main geoclimatic zones identified (Continental, Oceanic and Mediterranean).

b. Cold. The second main abiotic stress of faba bean is frost and in general winter conditions. The currently used winter-hardy material is of restricted genetic breadth. Recollecting winter-hardy types in promising areas or re-analysing *ex-situ* collections for winter hardiness should be conducted (Hu *et al*., 2010; Mikic *et al*., 2011). Winter faba beans are different from the autumn-sown faba beans arround the Mediterranean Basin (Flores *et al.*, 2012) which are challanged only by mild winters.

Summing up, the most important breeding objectives specifically for winter faba beans are (Link *et al.*, 2010) (i) high frost tolerance after hardening; (ii) appropriate hardening requirement, hardening effect and dehardening behavior; (iii) basic frost tolerance before hardening and after dehardening; (iv) adequate vernalization requirement; (v) field resistance of long snow-cover; (vi) high tolerance to frost-drought (*'Frost-Trocknis'*; winter drought; winter desiccation from high solar radiation during soil water is frozen); and (vii) tolerance of soil movement caused by cycles of frost and thawing (root rupture). The items after the first-mentioned one make up the main difference between frost tolerance assessment in controlled conditions and field-based breeding for winter survival. To tailor developmental rhythm of the plant to its target environment, we must look at vernalization and hardening together. Lee *et al.* (2001) showed for thale cress that both phenomena are to some extent genetically connected, yet Soja and Steineck (1986) reported them to be disconnected for faba bean. The major impact of an appropriate, vernalization-based postponement of flowering until after winter in pea is demonstrated by the *Hr*-locus, being a major frost-tolerance gene (*Hr*; Lejeune-Henaut *et al.*, 2004, 2008; Taye *et al.*, 2013). However, no such results are as yet available for faba bean.

European winter faba beans can be vernalized as seed or juvenile plants at non-freezing temperatures below about 10°C (Herzog, 1988). Yet, spring-sown winter faba bean, being unvernalized, respond to the long-day trigger and flower, albeit later (Ellis *et al.*, 1988a; Fujime *et al.*, 2000). Currently we see fast progress in the understanding of 'flowering genes' such has FLC and others (http://www.flowercrop.uni-kiel.de/en).

Optimum temperature for hardening is at about 5-8°C in the day and 2°C in the night, with sufficient light at day, whereas above 7°C already dehardening may start (Herzog, 1988). Hardening leads to cell membrane lipid unsaturation and changes in lipid to protein ration (Hughes and Dunn, 1996). Arbaoui and Link (2008c) found faba bean leaf lipids to be significantly decreased in oleic acid content, accompanied by a significant mean increase in linolenic upon hardening. Similarly, Collins *et al.* (2002) found a significantly higher level of unsaturated fatty acids in white clover genotypes that survived a frost test, than in the unselected population. Hardening increases the content of osmoprotectants that can accumulate without disturbing metabolism and protect against dehydration. Examples are proline, glycinebetaine and related compounds, specific sugars and some specific proteins (Uemura *et al.*, 2006).

Proline accumulation due to hardening is correlated with frost tolerance in faba bean (Arbaoui *et al.*, 2008a). Similarly, Konstantinova *et al.* (2002) found increased freezing tolerance in transgenic tobacco that accumulated proline. Verification of glycinebetaine as osmotic protectant in cool-season pulses is still lacking (Stoddard *et al*., 2006).

Duc and Petitjean (1995) and Arbaoui *et al.* (2008a) positively stated that results of controlled frost tests, for instance with potted juvenile plants in growth chambers, agreed with overwintering in the true field situation. Our current experience (Link and Sallam, 2013, unpublished) says that high frost tolerance in controlled conditions is a strict requirement to good survival of harsh winters, yet, is no sufficient guarantee. Obviously and understandably, there are furthers factors acting in the field (such as winter drought and soil movement (frost heaving by repeated freezing and thawing of soil; see above).

Central European winter faba beans such as the Göttingen Winter Bean Population, the cvs. Hiverna, Husky, Nordica, Diva, survive field temperatures down to −15 or −16°C if adequately hardened. At Göttingen, meanwhile further gain from selection for tolerance in controlled conditions was realized (Link and Sallam, 2013, unpublished; http://www.uni-goettingen.de/en/48273.html).

A common feature of drought and frost stress is water loss. Under frost, water moves from the cells into intercellular space (Thomashow, 1998). This water is found as ice crystals in the intercellular space. Ice crystals hurt cell membranes, and after thawing, hurt cells loose turgor and may die. Solutions to this threat, realized by some plant species and genotypes are ‘avoidance of ice formation,’ for instance via ‘depression of the freezing temperature by osmotic adjustment,’ and ‘supercooling below the freezing point,’ employment of ‘antifreeze proteins’ (Nilsen and Orcutt 1996; Thomashow 2001; Reyes-Díaz *et al.*, 2006; Uemura *et al.*, 2006). The existence and impact of such phenomena in faba bean are barely known.

Birch *et al.* (1985) reported superior frost tolerance of accession of *V. narbonensis* and *V. johannis*. Yet, with interspecific hybridization being unsuccessful, so far all attempts to exploit the secondary gene pool of faba bean failed. Duc and Petitjean (1995) found high and favourable heterosis for tolerance of potted, juvenile plants. This is corroborating our own findings (unpublished data) at Göttingen. Yet, heterosis can only partly be exploited in synthetic cultivars, because not hybrid cultivars are yet on the market (Link, 2009).

Molecular genetic work on frost tolerance was started and is in the pipeline. Arbaoui *et al.* (2008b) analyzed a set of recombinant inbred lines for frost tolerance, putatively uncovering three useful QTL for frost tolerance.

E. Forage Legumes

Forage legumes are key components of livestock operations whether grazed or harvested as hay or silage. Most forage legumes important to agriculture are perennials or annuals belonging to the *Medicago*, *Trifolium* and *Lotus* genera. Although several other forage legumes are adapted to and grown in different environments, alfalfa, also referred to as lucerne, is the most predominant forage legume grown worldwide. Alfalfa is a high-yielding perennial species with the capacity to adjust or adapt physiologically and morphologically over a certain range of temperature and rainfall to persist for a few years or from generation to generation over a period of years. The range of adaptability is genetically controlled and thus most species perform well in a characteristic region or adaptation zone. Cultivated alfalfa, an outcrossing autoteptraploid (2n = 4x) species, can be harvested multiple times in each growing season, is highly nutritious and an integral component for the beef and dairy industries. In addition to its broad economic value, alfalfa also has the capacity for symbiotic nitrogen fixation.

Forage legumes differ from seed legumes in the relative significance of vegetative leaf tissue, especially under a grazing system that requires a continuous supply of vegetative production. Although some forage crops are grown on soils ideal for agricultural, most forage species are grown on weathered soils that might be shallow, sandy, have fertility issues or those that have low water-holding capacity. Management techniques can be used to mitigate the effect of climatic constraints or stresses to extend the areas where desirable genotypes can be grown economically (Baron and Belanger, 2007). However, unlike annuals, perennials are long-lived and thus will likely encounter multiple impediments to plant growth and crop production during their lifespan. These limiting factors include abiotic stress conditions that account for extensive losses in agriculture. For a more detailed review on general forage legumes breeding please refer to Annicchiarico *et al.* (2014, this issue).

1. *Abiotic stress responses*

Increased demands for food production to feed a growing global population have pushed agricultural systems towards marginal lands. This shift in agricultural production will require the development of forage legume cultivars adapted to less-than-optimal conditions. Environmental factors that negatively affects plant growth and development represents a *stress*, and these stressors include limited water availability, temperature extremes, nutrient deficiencies, soil acidity and salinity. Usually one type of stress is accompanied or followed by another stress. For example, heat stress is accompanied by drought stress due to the physical loss of water and/or high atmospheric evaporative demand, and freezing stress is followed by drought stress due to the physiological unavailability of water (Agarwal and Zhu, 2005).

a. Drought. Erratic rainfall patterns have reduced agricultural productivity while areas in which fields are irrigated are at increased risk for salinization of field soils. Increased demands for water have also pushed agricultural systems towards rain-fed systems, further reducing forage biomass yield. Given the uncertainty over future water supplies in the realm of climate change (MacCracken, 2008; Erigayama *et al.*, 2009) and the increasing demand for water for non-farm use, increased water use efficiency (WUE) reflected in the amount of biomass produced per unit of water used, is an important trait for alfalfa improvement. Ecologically, the best strategy for plants during water deficit is to conserve their resources. From an agronomic perspective, the ideal tolerant plants would be able to continue to grow as if unaffected by drought. In the case of perennial legumes, survival during drought and the subsequent forage production following drought is an important component of the tolerance response. Agricultural management practices can be used to mitigate additional stresses on forage plants during grazing due to the effects from defoliation. Other strategies to enable better drought adaptation include the availability of soil nutrients (fertilizers) in adequate amounts to promote healthy plants and the development of vigorous roots (Blevins and Barker, 2007).

Alfalfa is characterized by a deep taproot that can grow to a depth in excess of 7 m (Humphries and Auricht, 2001), thus enabling it to grow in areas ranging from 250 – 1500 mm annual rainfall. Genetic variation was identified among and between alfalfa populations in response to drought and WUE, which indicates the amount of forage and root biomass produced per unit of water transpired (Ray *et al*., 1998, Ray *et al*., 2004; Han *et al*., 2007). Alfalfa genotypes contrasting for biomass production under various water regimens were used to identify QTL for biomass production under both irrigated and drought conditions (Han *et al.*, 2008). The alfalfa genotypes contrasting for drought response were further characterized for molecular, biochemical, morphological and physiological modifications. Changes in stomatal density, greater root growth following water withholding, greater accumulation of osmolytes, including raffinose and galactinol, and flavonoid antioxidants were observed (Kang *et al.*, 2011). Osmotic adjustments results in the accumulation of nutrients and sugars to change the cell water volume (Blevins and Barker, 2007) and these changes have been associated with tolerance to drought stress. Others reported a reduction in photosynthesis in response to water deficit in mature alfalfa plants (Bell *et al.*, 2007). Although increased cuticular wax accumulation in leaves enhanced drought tolerance (Zhang *et al.*, 2005), the wax contents in alfalfa leaves and their responses were not consistent when multiple alfalfa cultivars were evaluated (Ni *et al.*, 2012), suggesting this may be a genotype-dependent strategy to cope with drought stress.

Genes encoding transcription factors and other regulatory proteins, and genes involved in the biosynthesis of osmolytes and flavonoids were differentially regulated between two contrasting genotypes (Kang *et al.*, 2011). *WXP1* is an example of a transcription factor that leads to improved drought tolerance when overexpressed in transgenic alfalfa (Jiang *et al.*, 2009). The transgenic alfalfa lines showed higher net photosynthetic rate, transpiration rate, and stomatal conductance and higher efficiency of photosystem II, quantum yield of photosystem II and coefficient of photochemical quenching under water stress and in response to re-watering. The transgenic lines also showed higher relative water content and leaf water potential under water deficit conditions. In white clover, another important forage legume, the *WXP1* transgenic lines had higher net photosynthetic rates, higher relative water content and leaf water potential under drought-stressed conditions and overall improved tolerance to drought stress (Jiang *et al.*, 2010). Other transgenic approaches aimed at improving plant drought responses include over-expression of superoxide dismutase (McKersie *et al.*, 1996) and trehalose-6-phosphate synthase/phosphatase (Suarez *et al.*, 2009). Additional efforts to improve the WUE of forage legumes via traditional breeding approaches or genetic modifications can target various key processes: (a) mobilizing more of the available water through the crop rather than it being lost due to evaporation from the soil surface or drainage beyond the root zone; (b) producing more biomass in exchange for the water transpired by the crop by improving the WUE; or (c) partitioning more of the biomass into the harvested product (Condon *et al.*, 2004).

b. Heat tolerance. Alfalfa grows under diverse environmental conditions. Nevertheless, temperature stress is one of the primary factors limiting its growth and expansion into new regions. High temperatures can inhibit growth, reduce yield and shorten the longevity of the stand (McKenzie *et al.*, 1988). In many alfalfa-growing areas, air temperatures may exceed 40°C. These temperatures are considerably above the 27°C temperatures established for optimal herbage growth. Temperatures not sufficiently high to kill cells may still inhibit growth, impair vigor and suppress production as a result of high respiration losses, reduced N fixation, reduced carbohydrate reserves in roots and crowns, or an increased resistance to CO_2 diffusion due to smaller cells and leaves (Delaney *et al.*, 1974). High temperatures also increase the rate of plant development and reduce the leaf/stem ratio and digestibility in alfalfa (Buxton, 1996). Multiple biomass harvests combined with high soil temperatures can exacerbate the deleterious effects of heat stress (McKenzie *et al.*, 1988). The reduction of forage yield in alfalfa at high temperatures (and under limited water availability) is a complex process that cannot be ascribed to a single factor. Because breeding strategies aimed at enhancing drought tolerance will oftentimes capture the plant response to heat stress, heat tolerance is not considered by most breeders as an individual target for improvement.

c. Freezing tolerance. Forage legume breeders have emphasized temperature resistance, especially cold adaptation, for crown-forming perennials like alfalfa. Inadvertently though, the improved productivity under these conditions may be at the expense of winter hardiness (Beuselinck *et al.*, 1994). In general, as winter approaches, many plants acquire freezing tolerance during exposure to low, non-freezing temperatures during the cold *acclimation* process. The acclimation process that induces freezing tolerance in certain plant species is essential and often associated with a period of slow growth and dormancy (Mohapatra *et al.*, 1988). In alfalfa, specific cold acclimation or *cas* genes are expressed and metabolic changes occur (Monroy and Dhindsa, 1995). Vegetative storage proteins (VSPs) play adaptive roles in plant tolerance against freezing tolerance likely due to their antifreeze activity (Dhont *et al.*, 2006). These VSPs are also preferentially mobilized during alfalfa shoot growth in the spring or during regrowth after defoliation in the summer (Justes *et al.*, 2002). Alfalfa genotypes selected for higher autumn dormancy also showed a positive relationship between reduced winter injury and high total soluble proteins (TSP) concentrations in alfalfa roots (Cunningham *et al.*, 1998). The accumulation of endogenous carbon (C) and nitrogen (N) reserves in the roots of perennial alfalfa during autumn acclimation has an influence on the capacity of the plant to withstand winter stresses (McKenzie *et al.*, 1988; Volenec *et al.*, 2002) and the regrowth vigor during the following Spring (Dhont *et al.*, 2006). These findings provide insights into likely mechanisms of cold acclimation and freezing tolerance in alfalfa.

From a practical perspective, molecular markers targeting cold-inducible or cold-responsive genes can also be useful in breeding applications for cold tolerance. For example, a polymorphism in a cold-inducible dehydrin (highly hydrophilic protein) increased in frequency as a response to recurrent selection for superior freezing tolerance in alfalfa (Remus-Borel *et al.*, 2010). The progenies from crosses between contrasting genotypes also differed in their tolerance to subfreezing temperatures. Tetraploid alfalfa populations recurrently selected for superior freezing tolerance using an indoor screening method (Castonguay *et al.*, 2009) included positive alleles that enabled the identification of trait-related sequences with potential value for selection of alfalfa tolerance to subfreezing temperatures (Castonguay *et al.*, 2012). Although efforts for improving winter injury have been achieved and captured in more winter-tolerant cultivars, cold tolerance can also be affected by crop management strategies.

d. Soil pH and aluminum toxicity. Plant nutrition management plays a key role in the success or failure of alfalfa production. The composition, potential rooting volume and the previous application of soil amendments can affect the quantity and rate of nutrient availability. Non-optimal soil conditions for crop growth include nutrient deficiencies or toxicities due to metal ions that include the presence of available aluminum (Al) ions in acidic soils. A soil pH range of 6.6 to 7.5 is ideal for alfalfa production (McKenzie *et al.*, 1988). However, the optimum pH can vary with soil texture, organic matter and other soil chemical properties. Aluminum toxicity inhibits root growth and reduces yields due to insufficient intake of water and mineral nutrients (Kochian *et al.*, 2004). The growth of alfalfa plants at low pH decreases in the presence of Al due to reduced root growth (Khu *et al.*, 2012). Phenotypic screening methods that enable the dissection of acid-soil syndrome which consists of phytotoxicity to excess Al ions and protons were developed (Khu *et al.*, 2012) and used to identify genotypes with contrasting plant growth responses under these conditions. Although genetic variation in tolerance to soil acidity exists in alfalfa, it is generally less than that found in other crops and is yet to be deployed in alfalfa cultivars. Research aimed at identifying the genetic determinants underlying variation in alfalfa tolerance responses began with the identification of Al tolerance QTL based on biomass production and root growth of two populations (Khu *et al.*, 2013). Genes differentially expressed in response to Al stress in *M. truncatula* (Chandran *et al.*, 2008) and located within Al QTL intervals in alfalfa include those associated with cell wall modification, isoflavonoid biosynthesis, general stress responses and oxidative stress (scavenging of reactive oxygen species). Transgenic plants of several species overexpressing organic acid synthesis and/or organic acid transporter genes have shown enhanced tolerance to Al (Kochian *et al.*, 2004). Transgenic alfalfa expressing citrate synthase and a plasma membrane transporter showed higher Al and acid soil tolerance and lower levels of Al in shoot tissue than the non-transgenic isogenic population (Reyno *et al.*, 2013). These findings suggest that Al-exclusion could be driving Al and acid soil tolerance in the alfalfa populations evaluated so far. Current efforts aimed at enhancing productivity of alfalfa in acid soils also include evaluating the use of rhizobia strains tolerant to acid pH (Graham *et al.*, 1994) so as to enable symbiotic nitrogen fixation under acidic conditions and improve overall plant performance.

e. Soil salinity. Another major limitation to the expansion of forage legume production is the issue of soil salinity. Salt stress, particularly on irrigated land, has and will continue to reduce crop production in many parts of the world (Jenks and Hasegawa, 2005). Estimates suggest that 20% of the world's cultivated land and nearly half of all irrigated lands are affected by soil salinity (Rhoades and Loveday, 1990). High concentrations of salts cause ion imbalances and hyperosmotic stress in plants, including forage legumes. As a consequence of salt stress disrupting homeostasis in water potential and ion distribution at the cell and whole plant level, secondary stresses such as oxidative damage often occur (Zhu, 2001). The capacity of legumes to grow on saline soils varies among species and depends on the concentration of salts present in the rootzone and on various environmental conditions (Maas and Hoffman, 1977). Although alfalfa has been characterized as moderately sensitive to saline conditions with yield decreases proportional to the saturation extract salinity (Maas and Hoffman, 1977), it is more salt tolerant than other forage legumes including clovers (Munns, 2005). Progress from selection was made when seedlings were germinated under salt stress and further evaluated using callus cultures or whole plants (Scasta *et al.*, 2012). The biomass yields of alfalfa cultivars differ when grown in saline field conditions (Scasta *et al.*, 2012) and high fibrous rooting characteristics in alfalfa have shown some usefulness as a salinity stress avoidance mechanism (Vaughan *et al.*, 2002). These findings suggest that salinity problems can potentially be ameliorated through selection and development of salt tolerant cultivars. Although cellular and molecular responses to soil salinity have been identified (Hasegawa *et al.*, 2000), the specific mechanisms of tolerance to salinity in alfalfa are unknown. Initial evaluations suggest that alfalfa is able to regulate the uptake and translocation of ions to prevent excessive accumulation of these ions in the leaves (Munns, 2005). The development of salt-tolerant cultivars adapted to a wide range of environments combined with timely on-farm management decisions can contribute to profitable production of alfalfa on salt-affected soils.

2. Breeding approaches

Alfalfa cultivars are synthetic populations generated mainly through phenotypic recurrent selection. In contrast to the inbred and homozygous crop legumes, alfalfa cultivars consist of highly variable, heterozygous plants with complementary alleles. Long-term, traditional breeding programs to improve alfalfa yield under stress conditions are underway (Vasconcelos *et al.*, 2008; Li *et al.*, 2010). Breeding for broad spectrum disease and insect resistance should also continue to be a priority since these are likely to be more prevalent in environments under which abiotic stress is rampant. Moving forward, research aimed at identifying genes and tolerance mechanisms that are common both at the onset and during several abiotic stresses (Hirayama and Shinozaki, 2010) could be useful to breeders aimed at utilizing genetic markers targeting genes that enable a plant to increase (or at least maintain) biomass yields in multiple environments. Knowledge of the mechanisms underlying the activation and regulation of specific stress-related genes,the integration of molecular markers available in alfalfa (Han *et al.*, 2011, 2012; Li *et al.*, 2012) and genomic selection methodologies have the potential to accelerate the rate of genetic gains during each cycle of selection.

The development of perennial forage legume (alfalfa) cultivars that are able to thrive, persist and be productive under abiotic stress environments, can be used to bridge the gap between potential and realized crop yields and contribute to the implementation of sustainable agricultural systems worldwide.

F. Minor Grain Legumes

The term ‘minor’ is often used to characterize the range of plant species whose potential contribution to food security, health, income generation, and environmental services is not currently exploited due to their limited competitiveness with commodity-improved crops that are part of mainstream agriculture (Padulosi *et al.*, 2011). Indeed several of these species are grain legume staple crops grown in semi-arid tropics of Africa, Asia and South America (Varshney *et al.*, 2012b) and by being naturally exposed to various biotic and abiotic stresses, they are also being selected for increased resistance or tolerance.

Here we focus on four minor legume species representing the two main *Papilionoideae* subdivisions, to illustrate present achievements and challenges faced by minor legume species in relation to abiotic stresses. From the warm-season or tropical legumes (phaseoloid clade), cowpea and pigeonpea are included, and from the cool-season or temperate legumes (galegoid clade), lentils and grass pea were considered.

1. Abiotic stress responses

All of the four selected species are adapted to harsh environments with the presence of abiotic stress constraints. Cowpea is a widely adapted, stress tolerant grain, vegetable, and fodder crop grown in warm to hot regions of Africa, Asia, and the Americas, and to a lesser extent, in parts of Southern Europe (Ehlers and Hall, 1997). Pigeonpea is an important grain legume of the semiarid tropics and sub-tropics being grown in Asia, Africa, Latin America, and the Caribbean, since it is considered a hardy, widely adapted, drought-tolerant crop with a large temporal variation (90–300 days) for maturity (Varshney *et al.*, 2012a). Lentil is an annual legume crop that is produced throughout the world, and has special value in many of the semi-arid regions primarily due to its drought avoidance (Muehlbauer *et al.*, 2006). Finally, grass pea is a dual purpose (grain and forage) annual crop with a remarkable resistance to extreme environmental conditions (Vaz Patto *et al.*, 2006) and rightly considered one of the most promising sources of energy and protein for the vast and expanding populations of drought-prone and marginal areas of Asia and Africa. Due to its relative low input requirement, it is a model crop for sustainable agriculture and an interesting alternative for cropping systems diversification in marginal lands in Europe, Australia and America (Vaz Patto *et al.*, 2006; Almeida *et al.*, 2014).

All of these four species have considerable adaptation to drought. In pigeon pea, the ability to withstand severe drought is attributed to its deep roots and osmotic adjustment in the leaves. This species is capable of maintaining photosynthetic function during stress compared to other drought-tolerant legumes such as cowpea, and its unique polycarpic flowering habit further enables the crop to shed reproductive structures in response to stress (reviewed in Odeny, 2007). Additionally to its tolerance to drought, grass pea is also tolerant to excessive rainfall and can be grown on land subject to flooding. Its capacity to withstand moderate salinity has also been recognized (Campbell *et al.*, 1994). It has a very hardy and penetrating root system and therefore can grow on a wide range of soil types, including very poor soil, of fine texture, with neutral to alkaline pH, and heavy clays (Campbell, 1997). Grass pea has a high biological nitrogen fixation rate, which assists in maintaining soil fertility, and thus requires minimal production inputs (Campbell *et al.*, 1994). Cowpea also maintains adequate levels of SNF, effective symbiosis with mycorrhizae, and has the ability to withstand both acid and alkaline soil conditions what makes this legume tolerant to low soil fertility (Ehlers and Hall, 1997, and references therein). In this way, cowpea grows well even in poor sandy soils with low P levels (Singh *et al.*, 2003). Equally interesting is the high efficiency in P uptake of pigeonpea compared to other crops when grown on low P soils containing aluminum (Al) and its high tolerance to acid soils (Odeny, 2007, and references therein). Grass pea has been reported to be tolerant to a deficiency in essential nutrients and is able to store large amounts of lead in its root tissues (Brunet *et al.*, 2008), which could be a useful trait for new rhizofiltration systems.

2. Challenges due to abiotic constraints

Even though these four legume species show considerable adaptation to harsh environmental conditions, some abiotic stresses can nevertheless cause detrimental impacts on their production. As an example, cowpea suffers damage to reproductive processes when night temperatures exceed 20°C due to pollen sterility and indehiscence of anthers (Hall, 2004). Likewise, heat is also considered one of the most important stresses affecting lentil production worldwide (Muehlbauer *et al.*, 2006). Additionally both of these legume species are sensitive to chilling temperatures, exemplified by the reduction of cowpea's germination rate and final plant emergence when soil temperatures are below 19°C (Ehlers and Hall, 1997). Increased chilling tolerance at emergence in cowpea, as well as in lentil, especially in west Asia and North Africa regions and at high elevations (Muehlbauer *et al.*, 2006; Erskine *et al.*, 2011), would allow earlier planting in spring or even winter, and thus extend the growing season.

Similarly, salinity can also become a major problem for pigeonpea and lentil production especially under drought conditions in certain areas of Australia, Canada, and South and West Asia, and North Africa (Muehlbauer *et al.*, 2006; Odeny, 2007). Germplasm with tolerance to salt stress has been identified in cultivated lentil and also promising variation for tolerance to salinity was identified in wild related species such as *L. culinaris* ssp. *orientalis* or in several wild pigeonpea relatives (Erskine *et al.*, 2011; Upadhyaya *et al.*, 2013). Although cowpea is considered as an intermediate salt tolerant species salt stress can impose a multifaceted injury to cowpea plants particularly for seed germination, vegetative growth, and yield (Chen *et al.*, 2007). Nevertheless, significant variation was observed in this species for salt tolerance and thus it is likely feasible to select and breed for salt-tolerant cultivars.

Drought is considered one of the most important abiotic stresses for lentil production worldwide, as is the case for pigeonpea and cowpea particularly in its later stages of development (Muehlbauer *et al.*, 2006; Varshney *et al.*, 2010). Nevertheless, cowpea presents several broad adaptation mechanisms to drought. These include: drought escape, drought avoidance by decreasing leaf area or closure of stomata to reduce water loss and cessation of growth, dehydration avoidance, and vegetative stage drought tolerance by osmotic adjustment and continued slow growth or delayed leaf senescence (DLS) (Hall, 2004, and references therein). DLS allows the crop to remain alive through a midseason drought and recover when rainfall resumes (Gwathmey and Hall, 1992) and this adaptation mechanism appears to be conferred by a single gene involving resistance to premature death caused by *Fusarium solani* f. sp. *phaseoli* (Ismail *et al.*, 2000). Kulkarni *et al.* (2000) suggested that the intrinsic capacity of cowpea varieties for ABA synthesis could also play an important role in regulating stomatal conductance in a drying soil and provide useful selection criteria for tolerance to drought stress. However in the majority of the minor plant species, physiological studies to understand the mechanisms and physiological traits conferring abiotic stress tolerance are scarce. For instances, drought stress responses in grasspea were evaluated through ecophysiological parameters, such as water extraction, stomatal responses or water use efficiency (Silvestre *et al.*, 2014, and references therein). Nevertheless, a recent report suggested that improved drought tolerance in grass pea can be correlated with an increased accumulation of proline and soluble sugars together with improved strategies to dissipate reactive oxygen species under stress conditions (Jiang *et al.*, 2013). Additionally, the lack of adequate screening methodologies, account for the under utilization of drought resistance traits from this minor legume species broadly in legume breeding programs. Recent advances in the development of efficient methods to screen for abiotic stress responses were implemented in the development of large scale *Lathyrus* drought and salt stress screening methods (Talukdar, 2011; Silvestre *et al.*, 2014).

Soil imbalance in key minerals such as iron and boron constrains lentil yield similarly to the reduced productivity in pigeonpea from Al toxicity (Choudhary *et al.*, 2011; Erskine *et al.*, 2011). However, these stresses remain of local importance and variation exists within the cultivated germplasm. For instances, germplasm screening indicates that tolerance to iron deficiency is common among lentils from Syria and Turkey and landraces from Nepal and Bangladesh were identified as tolerant to boron deficiency (Erskine *et al.*, 2011, and references there in). Furthermore, Al tolerant pigeonpea accessions have been consistently discriminated from sensitive genotypes using a rapid method based on hydroponic or sand assay seedlings growth response traits (Choudhary *et al.*, 2011), with tolerance attributed to the exclusion of aluminum from the root.

Finally, water logging during the early developmental stages is an important constraint for pigeonpea and lentil production (Erskine *et al.*, 1994; Varshney *et al.*, 2010). Nevertheless, lentil genotypes that are more resistant to flooding were identified and these are characterized by large aerenchyma or air-spaces in their roots and by higher stomatal conductance compared to the more sensitive ones (Stoddard *et al.*, 2006, and references therein). The highly flood resistant grass pea does have one important constraint that might be related to its higher survival rates under harsh conditions. Grass pea contains a toxic non-protein amino acid (β-ODAP, β-N-oxalyl-L-α, β-diaminopropionic acid) (Campbell *et al.*, 1994) which levels were reported to vary in different tissues during plant development, and to be affected by a wide range of environmental stresses (Jiao *et al.*, 2011). Xing *et al.* (2001) speculated that β-ODAP could scavenger the hydroxyl radicals to protect glycolate oxidase activity under water stress. Nevertheless, the role of β-ODAP in *Lathyrus* genotypes is still unknown. From the existing literature it is unclear if the initial β-ODAP content of a particular genotype would influence its behavior under drought or other abiotic stress conditions, and if the β-ODAP accumulation can be correlated with improved resistance. The clarification of these particular aspects requires further studies.

3. *Breeding achievements*

The development of productive early maturing cowpea cultivars has been one of the major important achievements from breeding efforts aimed at enhancing drought stress tolerance and is based on one of the previously described cowpea broad adaptation mechanisms (Ehlers and Hall, 1997). Early maturing cultivars can escape the end-of-season drought occurring in semiarid zones. Taking this into consideration, Hall (2004) considered that breeding should focus on two types of cultivars and these should be grown simultaneously to enhance the likelihood that significant grain production would be achieved every year. One type would be the early maturing with synchronous flower production, and the other type would began flowering later, with a more sequential rather than synchronous flowering. Accordingly, whereas the first cultivar type, if exposed to intermittent drought during the vegetative or reproductive stages would perform poorly, the second type, exhibiting greater resistance to midseason drought, would survive, but with a diminished ability to escape late-season drought.

Drought escape has been implicated on lentil adaptation to drought through early flowering, early growth vigor and rapid root growth (Erskine *et al.*, 2011). Useful genetic variation was reported in response to drought stress within the lentil cultivated germplasm and variation has also been noted within wild *Lens* species particularly *L. culinaris* ssp. *orientalis*, often found in habitats receiving low average rainfall (Erskine *et al.*, 2011). In particular, drought tolerant lentil cultivars exhibit lower cell-membrane injury and higher seedling growth, osmotic regulation and higher WUE (Stoddard *et al.*, 2006).

In relation to heat stress, cowpea tolerant germplasm has been developed that is effective in both long-day and short-day conditions (Ehlers and Hall, 1997). Tolerance to heat-induced suppression of floral buds appears to be conferred by a major recessive gene, whereas the ability to set pods under hot conditions is controlled by a single dominant gene (Ehlers and Hall, 1997, and references therein). A close relationship between heat tolerance during pod set and slow electrolyte leakage from leaf discs subjected to heat stress was identified and this was used as a rapid method for heat tolerance screening (Hall, 2004). In cowpea, chilling tolerant germplasm was identified and the dehydrin protein seems to confer an incremental tolerance based on single nuclear gene inheritance (Hall, 2004, and references therein).

As previously mentioned, cowpea and lentil production can be increased significantly by shifting sowing from spring to early spring or winter (Ehlers and Hall, 1997; Erskine *et al.*, 2011), only if the cultivar is winter hardy. Considerable variation for winter hardiness and cold tolerance was identified in lentil cultivated germplasm and also among wild relatives (Erskine *et al.*, 2011). The inheritance winter hardiness in lentil was described as polygenic and QTL mapped (Kahraman *et al.*, 2004a, b). Molecular markers associated with these QTL could be used in a marker assisted selection (MAS) program for winter hardiness after being validated and could include the use of the microsatellite marker ubc808-12 (Muehlbauer *et al.*, 2006). Eujayl *et al.* (1999) also identified a RAPD marker (OPS-16750) that could be useful for MAS due to its linkage to a dominant seedling frost tolerance gene, Frt.

Until recently another factor that limited the improvement of abiotic stress resistance in some of these minor legumes was the limited number of genomic resources available (Varshney *et al.*, 2012a). Nevertheless, presently many minor legumes are becoming "genomic resources rich crops" (Varshney *et al.*, 2009). For example, a genome sequence is now available for pigeonpea (Varshney *et al.*, 2012a). Cowpea genomics is also progressing and several QTL associated with seedling drought tolerance, based on maintenance of stem greenness and recovery of dry weight (Muchero *et al.*, 2009), were identified. Several gene-derived markers that co-segregate with these QTLs were developed (Muchero *et al.*, 2010). Additionally, more than a dozen genes associated with drought stress response were cloned and characterized (Muchero *et al.*, 2010, and references therein). However, the specific role of these genes remains unknown. Additional resources in cowpea include numerous miRNAs that were identified under saline stress conditions using a homology searches based on cowpea miRNAs that are conserved in other plants (Paul *et al.*, 2011). Likewise, Barrera-Figueroa *et al.* (2011), identified miRNAs that may play important roles in drought tolerance and may be key factors in determining the level of drought tolerance in the different cowpea genotypes. Further characterization of the targets of abiotic stress-associated miRNAs will help understand mechanisms of stress tolerance in cowpea.

Promising results are being obtained through MAS for lentil disease resistance genes and the same molecular breeding achievements are expected for abiotic stress resistance improvement in the near future given recent efforts in transcriptome profiling in this species (Sharpe *et al.*, 2013). In the case of grass pea, although progress was achieved in obtaining genomic information from the *Lathyrus* genus, these resources are still comparatively modest. Nevertheless, the marker technologies with cross amplification in different species (Almeida *et al.*, 2014) and the gene expression analyses in *Lathyrus* (Vaz Patto *et al.*, 2011) allowed the identification of gene-specific molecular markers for the construction of high-density genetic linkage maps. These enhanced maps will facilitate the localization of useful abiotic stress resistance genes and QTLs for grass pea MAS, with the possibility of alignment with other species thus providing opportunities to use interesting abiotic stress resistance from grass pea in other related species.

CONCLUSIONS

In many regions of the world, especially under more marginal conditions, legumes play an essential role in enhancing food security, and promoting the development of a range of economic, social and environmental benefits. Like in many other crops, legume cultivation and productivity is affected by abiotic constraints, and the threatening aggravated scenario imposed by climate changes (IPCC, 2012) highlights the need for a globally concerted research approach. A collective research approach will facilitate the development of legumes (and other crops) that are able to adapt to and be productive under environmental limitations thus increasing yield and quality under abiotic stress and thus contributing to the implementation of a sustainable agricultural system.

Advances in genomics and the development of breeder-friendly toolboxes have revolutionized plant improvement strategies by integrating complex biological data to inform genome-assisted breeding approaches (Wang *et al*., 2013). From this review we can conclude that model legumes have provided a valuable resource for translational approaches aimed at dissecting the molecular and physiological responses to abiotic stresses. By utilizing the genomic resources and high-throughput technologies available, genes associated with plant abiotic stress response(s) were deployed to generate stress tolerant legumes, via conventional and novel molecular breeding approaches. Nevertheless, research on abiotic stress resistance in legumes has mainly been conducted using discipline-specific or single gene based approaches, despite the level of complexity and complementarity observed (Table 1). The emphasis has shifted to the translation of the information gained in model systems in controlled environments to crops or forages in field conditions characterized by the simultaneous occurrence of different abiotic stresses. The research developed using soybean, as a model crop species, is one relevant example of successful translational research undertaken. The use and development of methodologies based on System Biology approaches will circumvent the barriers that previously blocked the translation of knowledge to generate new crop genomic resources (Cramer *et al*., 2011). Additional opportunities for the genetic improvement of abiotic stress tolerance in both grain and forage legumes include harnessing post-transcriptional gene regulation (Sunkar *et al*., 2007) and the corresponding databases to explore miRNA-abiotic stress regulation including miRBASE (Kozomara and Griffiths-Jones, 2011) and *PASmiR* (Zhang *et al*., 2013). Moreover, the emerging innovative high-throughput phenotyping strategies provide the opportunity to assess spatial and dynamic differences in abiotic stress resistance traits relevant to the field performance of legumes (Tuberosa, 2012; Claeys and Inzé, 2013; McAusland *et al*., 2013). The combination of multiple complementary strategies should be an integral part of legume improvement strategies and is expected to enable researchers and breeding to more efficiently address the current and future demands of modern agriculture and food production presently exacerbated by the variability in global climate change.

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