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Chapter

Drought Stress Response in Agricultural Plants: A Case Study of Common Bean (*Phaseolus vulgaris* L.)

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Abstract

Drought is one of the major threats to common bean (*Phaseolus vulgaris* L.), affecting its growth and productivity and, thus, contributing to considerable losses in yield in many regions worldwide. The development of varieties tolerant of drought stress has, therefore, become one of the primary goals in many common bean breeding programs. Plants have developed various mechanisms of their adaptation, to a greater or lesser extent, to drought. These are expressed, on the molecular level, by changes of gene expression and of protein content, together with responses at physiological and morphological levels. The response of common bean to drought is still not sufficiently well characterized due to its genetic complexity and its diverse, often ambiguous, phenotypic effects. Understanding these mechanisms is thus of fundamental importance for developing varieties that are better adapted to such stress conditions. In this chapter, we present research that provides an insight into the morpho-physiological adaptation and its underlying molecular changes in common bean plants exposed to drought. We include our contribution to establishing the basis for breeding of common bean with greater tolerance to this abiotic stress that uses molecular markers and identification of quantitative trait loci (QTLs).

Keywords: common bean, drought, transcriptomics, proteomics, posttranslational modifications, quantitative trait loci (QTLs), breeding

1. Introduction

Common bean (*Phaseolus vulgaris* L.) is cultivated worldwide and accounts for one-third of cultivated legumes (FAOSTAT, 2014). The biggest producers are Brazil, USA and Mexico, while millions of tons are produced annually in Africa. Its high levels of protein and carbohydrate make common bean a staple in food, and it is an important source of vitamins and minerals, including iron, magnesium, potassium, zinc, selenium and calcium [1–4].

It requires a considerable amount of water during its growing season in order to develop and produce seeds in accordance with its genetic potential [1, 5]. Exposure to drought can thus result in diminution of fitness, quality and quantity of yield,

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depending on the timing, intensity and duration of drought, as well as on the stage of development of the exposed plant. Exposure to drought stress can be fairly constant throughout the season or may affect plants in a specific stage of their life cycle, thus delaying early plant development, vegetative growth, flowering and/or maturation [6]. In the most arid areas, annual losses of common bean yield can exceed 60%, rising to 80% at the height of the drought [5–7].

Plants have, during evolution, acquired different modes of adaptation to harsh environmental conditions, including drought stress [5, 8, 9]. Some plants escape the latter by early maturation and, in consequence, more rapid development of seeds, thus completing their life cycle before the onset of prolonged and severe drought. Others have developed morphological, anatomical or physiological adaptations that enable them to maintain high water potential during drought (drought avoidance), or mechanisms directed to survival in the presence of low water potential (drought tolerance). Adaptations leading to drought avoidance include increased density of roots and their deeper propagation that enables more effective water absorption from the soil, and decreased leaf area and stomata closure that control the limitation of water loss through transpiration [10]. Drought tolerance is based on tissue- and cell-specific physiological and molecular adaptations such as synthesis of osmoprotective proteins like dehydrins and chaperons [11–13].

An outstanding characteristic of common bean germplasm is its particularly high diversity. In the second part of this chapter, the general picture obtained by commonly used screening methodology is presented. This includes phenotyping of phenological, anatomical and morphological, as well as yield associated traits, illustrating this diversity with the aim of pointing out that common bean responses to drought can differ greatly between specific genotypes. An example of this approach is that phenotyping of American genotypes in the last decades led to the discovery of important drought resistance sources from the Mesoamerican gene pool, largely belonging to the race Durango, thus forming the basis for numerous subsequent studies [5]. For such reasons, continuous efforts are devoted to screening common bean germplasm for more drought resistant genotypes that exhibit different, and potentially complementary, drought resistance traits that are and will be used to study and better understand the mechanisms of resistance and for the breeding of new varieties.

The plant response to drought results from complex and diverse adaptation. It has, therefore, to be studied on levels ranging from morphological and physiological changes observed in organs to the intricate responses on the gene expression and regulation levels and to biochemical responses on the level of cells and organelles [12]. In the present chapter we therefore focus further on the physiology of the response of common bean to drought, followed by a survey of research on the influence of drought on its transcriptome, proteome and post-translational modifications.

In the last part of this chapter the genetic level is considered, disclosing drought response as a complex quantitative trait controlled by a number of major and minor genes clustered on specific loci, as well as several genomics and molecular approaches that have been utilized for their study [14]. For common bean genotyping and for subsequent mapping of quantitative trait loci (QTLs) a large variety of genetic markers, from simple sequence repeat (SSR) to single-nucleotide polymorphism (SNP) markers, are now available, enabling use of this approach in identifying molecular markers of tolerance to drought.

Further, identification of genes that are expressed differently under drought conditions from that in well-watered plants, especially if contrasting tolerant and sensitive genotypes, may also lead to the discovery of specific markers that can be used in breeding. Similarly, protein markers can be discovered by proteome

profiling studies by identification of differentially expressed proteins in regard to the drought conditions or genotype sensitivity to drought [15–17]. All further attempts at successful breeding of common beans with improved tolerance to drought will benefit greatly from the determination of the genome sequence of common bean that has enabled the development and identification of novel molecular markers and completion of a comprehensive common bean consensus map applicable to both Andean and Mesoamerican genotypes [18].

2. The diverse common bean germplasm as a potential for discovering new drought-responsive traits

Common bean originates from Mexico and was separated in two ecologically and geographically different Mesoamerican and Andean gene pools [19, 20]. Mesoamerican bean genotypes can be distinguished by longer flowering times and small seeds, while Andean genotypes have large and colorful seeds [21, 22]. Phylogenetic studies and evaluation of common bean genotypes collected from different regions, ranging from the Americas, Africa [23, 24] and Europe [25–28], have confirmed independent domestication events specific to each of the gene-pools [20, 29].

Common bean was introduced in Europe centuries ago by independent domestication events from both major centers of origin [25–28]. Our phylogenetic studies shed more light on the understanding of dissemination pathways and the evolution of this species in central Europe and have been focused on the germplasm from the Central European, South East European and Balkan region [27, 28, 30]. Evaluations of genetic diversity and the population structure of 167 historical and current accessions with the different geographical origin (Slovenia, Austria, Bosnia and Herzegovina, Croatia, Macedonia and Serbia) have revealed great allelic polymorphism in 14 SSR markers. The strong predominance of Andean genotypes in Slovenia and several Western Balkan countries indicates their introduction from the Mediterranean basin and countries such as Italy. On the other hand, a high proportion of Mesoamerican genotypes in the present Austrian germplasm (44%) could indicate their introgression from western and northern European countries driven by historical events.

Cultivation in diverse local environments and climate areas, ranging from lowlands to high altitude regions in equatorial and more temperate climate conditions have contributed to the high diversity of common bean in terms of growth type, seed properties and maturity time [31]. Consequently, the diverse common bean germplasm represents an important trait pool for searching for new traits such as abiotic stress tolerance traits [31]. The screening process is largely based on phenotyping genotypes exposed to a form of drought, with possible subsequent rehydration in comparison to irrigated conditions. It is usually performed in different locations, over several seasons, either in the field or in controlled greenhouse conditions. Screening commonly includes phenotyping of phenological traits such timing of flowering and maturation, anatomical and morphological traits describing plant fitness and yield-associated traits as a measure of the effect of drought on yield output.

In the past decades, considerable efforts have been made to characterize the American germplasm for different traits including drought responsive traits [5]. The identified drought resistance sources of race Durango have become a cornerstone for research of complex drought tolerance mechanism and introgression of traits into the cultivars.

Another example is Central and East European common bean germplasm that consists of thousands of collected genotypes deposited in the national and regional gene banks and preserving this variability is an important step in preventing gene erosion,

as well as supporting breeding programs with genotypes showing different environmental adaptations. Characterization and evaluation of this germplasm are an ongoing process and have confirmed the very broad genetic diversity of common bean in Eastern Europe. Our recent proceedings have resulted in formation of a core collection having applicative value for direct breeding purposes [32]. Screening for representative genotypes for core collection included initial evaluation of basic multi-crop passport descriptors (e.g., geographic origin, biological status, and ancestral data), phenotypic seed characteristics and phaseolin type, as well as assessment of genetic structure by genotyping with genetic markers. The resulting core collection encompasses 63 accessions representing the global genetic diversity and 14 standard genotypes with desirable traits from the East European region (unpublished data) and was evaluated under field conditions as well as for the presence of genetic markers associated with traits of interest and biochemical analysis. Core collection was further evaluated for agronomic traits in field conditions (response to abiotic stress), genetic markers for desirable traits and nutritional traits of importance (multi-elemental composition, fats, proteins, and phytic acid). These results enabled selection of superior genotypes in core collection for further breeding applications.

3. The physiology of drought response

The observed physiological changes in plants exposed to drought can be a direct consequence of drought, as well as of the response of the plant, in order to mitigate the stress. Drought typically occurs as a result of low and non-frequent precipitation, resulting in reduced soil water content that is first detected by plant roots [33]. Depending on drought duration and severity the water status of plants can be affected by insufficient water absorption due to low soil water availability, as well as to increased water loss in the process of transpiration. Water deficit in plants affects their normal physiological processes and hinders the development, growth and yield, ultimately resulting in wilting, senescence and plant death [33]. Drought can be potentiated by heat stress, which propagates the water loss from the plant by increased water evaporation from the leaves, and by soil salinity stress, together reducing soil water availability as well as having an additional toxic effect on the plant [34–36].

Drought responsive traits have been studied in common bean by evaluating various traits in field experiments as well as in more controlled environments, such as, greenhouses [37]. Phenological and yield-associated traits have been studied frequently because they are affected by drought stress, are an important indicator of yield output and are also measurable in a large phenotyping population. Phenological traits can also represent the adaptation of the life cycle of a plant to specific drought conditions in the environment. Breeding for earliness is an effective strategy for increasing the yield stability in regions such as the Mediterranean, where plants are exposed to increased drought in the summer time. Early flowering can help in drought avoidance; however, it is not effective in mitigating the drought stress once it occurs [9].

The response to drought in different common bean genotypes has been characterized in several studies based on physiological measurements such as photosynthesis and photosynthate acquisition as well as on partitioning indices [5, 38–44]. Photosynthesis and cell growth are primary processes influenced by drought due to decreased stomata conductivity in the early drought phases that limits evaporation and CO_2 diffusion in the leaf mesophyll. The surplus of energy on the thylakoids in the photosynthesis apparatus results in photo inhibition—reduced photochemical efficiency [45]. Stomata closure is an effective strategy for shorter drought periods and for mild drought where photosynthesis is not affected in such a way as to reduce

the yields [38]. When the duration of drought is longer, better drought tolerance and yields are enabled by a specific biochemical mechanism on the cell level. High yields of tolerant Durango genotypes, such as, 'Pinto Saltillo,' exposed to drought have been associated with early and fine regulation of the stomata response and with CO_2 assimilation with stomata closure, limiting water loss during the day, maintaining higher relative water content (RWC) at night, with increased water use efficiency and limitation of reactive oxygen species (ROS) accumulation [41, 42, 44].

Screening selected genotypes adapted to Central European climatic conditions enabled us to identify genotypes with more drought tolerant traits [46, 47] thus becoming a starting point for studies on the mechanisms of drought. They were performed under controlled conditions with drought being induced by discontinuing irrigation and assessment of drought by soil water potential measurements. Observation of plant physiological changes, measurements of leaf water potential, relative water content and yield were employed for determining drought tolerance. Among the tested cultivars adapted to the growing conditions of the Central European region, the greatest difference in response to drought was observed between 'Tiber' and 'Starozagorski Čern,' the former being the most tolerant. For this reason these two cultivars were used in many of our studies of the response to drought [46, 47]. Studies on the level of physiology have confirmed that the ability to withstand drought is also related to the water consumption pattern of the plant. Some cultivars such as 'Starozagorski Čern' exhibit water spending behavior that enables them to thrive, and, when the water supply is sufficient, they produce high yields [47]. However, when exposed to drought, their yield can be significantly reduced. In contrast, cultivars adapted to harsher environments, regulate water more conservatively and their yield during drought is affected less, as is the case with 'Tiber.' Drought tolerance in water saving cultivars has been associated with great plasticity on the biochemical and cellular levels, being associated with stomatal conductance, photosynthesis rate, abscisic acid (ABA) synthesis and resistance to photoinhibition [39]. In addition, the distribution of photosynthetic products to developing pods and seeds is an important factor in determining the yield under stress, with genotypes with better partitioning indices expressing a higher yield [5, 40, 43].

4. Response to drought on the molecular level

Understanding the changes in metabolic pathways in plants under the influence of drought, as well as the molecular mechanisms regulating their adaptation to this stress, is very important in identifying key molecular markers that could help distinguish between genotypes with different tolerance. On the molecular level, drought affects plant cells in different ways—through changes in gene expression and/or translation of transcripts to proteins, through posttranslational modification leading to protein activation and by further direct action on the protein itself. It is important to underline that these ways are interdependent and that only active key proteins enable a response beneficial for the plant.

Screening genes with differential expression and proteins with changed abundance or activity in plants exposed to drought is greatly facilitated by modern transcriptomic and proteomic tools which have, together with other approaches, enabled rapid development of the field. Identification of detected genes and proteins is greatly facilitated by the recent advances in sequencing and the publication of full genome sequences of model legumes *Medicago truncatula* [48] and *Lotus japonicus* [49] and of crop legumes, such as, common bean [50], soybean [51], chickpea (*Cicer arietinum*) [52] and peanut [53]. Comprehensive lists of genes and proteins obtained from screening studies are then classified according to their

known ontologies in order to further investigate their interactions and connections, by methods of bioinformatics and systems biology, into metabolic pathways. A combination of these approaches has enabled the identification of thousands of genes with differential expression and hundreds of proteins with changed abundance in common bean under drought [15, 17, 54–56] as well as other model, crop and forage legumes [57].

4.1 Transcriptomic profiling of drought response

Early transcriptomic profiling methods employed over the past decades utilized polymerase chain reaction (PCR) and hybridization techniques and allowed for detection of a smaller number of transcripts with a large difference in mRNA abundance between compared samples [58, 59]. Today these methods are being replaced by genome-wide profiling techniques, such as, microarrays and whole-genome mRNA sequencing (RNA-seq). Further intricacies of gene regulation are explored by profiling miRNAs, small non-coding RNAs that regulate gene expression [55, 56, 60–62].

The transcriptomic response of common bean has been investigated in various plant organs of different genotypes with respect to different stages of drought severity [56]. One of the first studies focused on roots, the first plant organ in which to detect changes in soil water content [55]. Several dehydration-related genes were identified that are associated with signaling, protein homeostasis and root growth modulations, among which a gene *PvOCT1*, encoding a new type of organic cation transporter in plants, has been reported [63]. The response in leaves is equally important since the regulation of transpiration plays an important role in the plant response to drought. We showed that in leaves of eight common bean genotypes at different levels of dehydration, up-regulation of transcription factors and genes encoding osmoprotectants, late embryogenesis abundant (LEA) proteins, protein kinases, aldehyde dehydrogenases and cell and carbohydrate metabolism-associated genes occurs, while several photosynthesis-related genes were down-regulated [58]. Only minor differences in expression of 15 studied genes were found between the studied cultivars. The similarity in the gene expression of different cultivars tested in the growth chamber and under greenhouse conditions supports the conclusion that the genes identified in response to water withdrawal constitute a general and intrinsic response of common bean to drought and strengthens the relevance of the experimental results to field conditions [58]. In a study on drought tolerant 'Long 22-0579' and drought sensitive 'Naihua' Chinese common bean cultivars, *de novo* assembly of transcriptome data enabled detection of more than nine thousand drought-responsive candidate genes differentially expressed between the drought and control treatments or between both cultivars exposed to drought [56]. Detected genes include those associated with drought-related metabolic processes (cell metabolism, cell wall and carbohydrate biosynthesis), osmoprotectants (proline), transcription factors (MYB, WRKY, DREB, and NAC), plant hormone regulation, signaling, and cell communication. The expression data enabled further characterization of drought responsive NAC transcription factors [64]. In the same two cultivars, 49 novel and 120 known miRNA were detected, 24 of them showing either increased or decreased expression during drought, and only four sharing the same expression pattern between the cultivars [58]. Among the target genes were genes encoding transcription factors, protein kinases and nuclear transcription factors.

Examples of studies aimed at identifying differences in gene expression of particular groups of genes are those focused on aquaporins (AQPs). These are membrane proteins controlling transcellular water movement from the roots and throughout the plant to assimilating tissues. For this reason, they are involved in controlling the ability of plants to regulate their water supply and transport which is closely related

to their ability to tolerate or withstand drought. In higher plants, AQPs form a large and diverse protein family with 35 homologs in Arabidopsis (*Arabidopsis thaliana*) and up to 71 homologs in cotton (*Gossypium hirsutum* L.) [65, 66]. In common bean AQPs with the highest mean expression during drought, as well as under normal conditions, were identified [67]. Expression of their genes has been investigated in genotypes with different responses to drought [47, 59, 68]. Increased expression of *PvTIP2;3* was reported in drought-stressed roots of the tolerant genotype [68] and up-regulation of *PvPIP2;5* in leaves of bean exposed to drought was correlated with a reduction in the transpiration rate [69]. In our recent study, physiological measurements indicate greater prevention of water loss in more drought tolerant cultivars, which may be associated with rapid and adequate down-regulation of AQPs in the plasma membrane and tonoplast [47].

4.2 Proteome analysis of drought response

Although studies of drought stress at the gene expression level provide many important data and indications, changes in the transcriptome do not necessarily mean that they will be translated into the proteome level. Studies using proteomic methods are therefore essential for revealing, not only the role of proteins in complex mechanisms of drought response in common bean, but also for pointing out possible molecular markers of drought tolerance. These methods not only enable identification of proteins with abundance changed in response to environmental stress, but also the detection of protein complexes and protein localization, as well as of post-translational protein modifications related to a specific stress factor [70–72] as reported later in this chapter. As underlined above, this approach has experienced rapid development by the recent publishing of full genome sequences of many plants, among them common bean [50].

One of the first studies of drought induced changes in common bean on the proteome was our research focusing on leaves and stems of two cultivars differing in their response to drought [15–17]. In 'Tiber,' we identified 58 proteins whose abundance changed significantly and in 'Starozagorski čern' 64 [15]. Most of the identified proteins were classified into functional categories that include energy metabolism, photosynthesis, ATP interconversion, protein synthesis and proteolysis, stress and defense-related proteins. Significant changes in abundance were observed in large proportion of proteins associated with photosynthesis, such as Rubisco, carbonic anhydrase, oxygen evolving enhancer proteins and chlorophyll a/b binding proteins. While Rubisco small subunit showed lower abundances in drought in both cultivars, carbonic anhydrase was reduced in 'Starozagorski čern,' and in 'Tiber' we detected both increased and reduced abundance. Abundance of chlorophyll a/b binding proteins increased in 'Tiber' and was reduced in 'Starozagorski čern.' The most outstanding contrasting abundance between the two cultivars was the oxygen evolving enhancer proteins, OEE1 and OEE2. Significant changes in abundance were observed in case of a few of the proteins involved in response to stress (e.g., superoxide dismutase, ascorbate peroxidase, and dehydrin) and in case of proteins associated with proteolysis and protein folding (e.g., cysteine proteinase CP2, precursors of cysteine proteinase, proteasome subunit beta type, peptidyl-prolyl cis-trans isomerase, and 20 kDa chaperonin). For peptidyl-prolyl cis-trans isomerase we detected higher abundance in 'Tiber' and reduced abundance in 'Starozagorski čern' under drought conditions. From the category ATP interconversion, in both cultivars nucleoside diphosphate kinase (NDPK) significantly increased under drought whereas ATP synthase decreased in abundance. Interactions between identified proteins were demonstrated by bioinformatics analysis, enabling a more complete insight into biological pathways and molecular functions affected by drought stress.

The further study on stem [16] carried out on cultivar 'Tiber' showed changed abundances under drought of proteins that can be classified in the same categories as leaf proteins. The proteins with increased abundance indicate the importance of maintaining protein homeostasis to mitigate this stress. There was increased abundance of proteins involved in protein synthesis, proteolysis and protein folding. Among them, the protein with the greatest abundance was 70 kDa heat shock protein that chaperones the correct folding of proteins [16].

4.3 Postranslational modifications in the response to drought

The complexity of the response of plants to drought is further emphasized by reports indicating that posttranslational modifications (PTMs) of proteins also play an important role. These include covalent modifications of a number of cell proteins that follow protein biosynthesis and are usually catalyzed by enzymes. There are different types of PTMs, among them glycosylation, that are recognized as being very important in plants and in their response to stress [73, 74]. This type of PTM affects protein stability, interaction with other proteins, protein trafficking and, as a consequence, protein activity.

Only a small number of the proteomic studies that have been carried out address specifically protein glycosylation and changes in abundance of glycoproteins in crops under abiotic stress [17]. One of them is our study of glycosylated proteins in leaves of common bean stressed by drought [17]. 'Tiber,' previously identified as relatively tolerant to drought [46, 47], was investigated. Thirty-five glycoproteins with changed abundance were detected. Their structures showed high mannose, complex and hybrid types of N-glycans, most of them being associated with the cell wall (many cell wall-degrading enzymes, such as, β-glucosidase, α-arabinofuranosidase and β-xylosidase, were more abundant under drought), with the stress response (such as, ascorbate oxidase, purple acid phosphatase and reticulin oxidase-like protein that were also more abundant) and with proteolysis and protein folding (such as, the precursor of subtilisin-like serine protease, nicastrin, the precursor of cysteine protease and protein disulfide isomerase that were less abundant) [17].

It follows from the studies reported above that proteome analysis of common bean under drought has revealed the participation of proteins involved in proteolysis [15, 17]. Many proteins, after their synthesis, need to be activated by highly regulated proteolytic cleavage of specific peptide bonds that removes parts of their peptide chains. Activation of regulated proteolysis and simultaneous inhibition of uncontrolled proteolysis are vital for cell survival under dehydration stress. All beneficial changes in metabolism under drought require the active involvement of controlled proteolysis that regulates the turnover rates of specific enzymes and/or proteins involved in cell signaling, and ensures degradation of oxidatively damaged, improperly folded and irreversibly denatured proteins [75, 76]. On the other hand non-specific, uncontrolled proteolysis can be damaging to cells, leading to random breakdown of the majority of cell proteins. Such protein degradation, provoked by drought, results mainly in the disruption of cell membranes and exhibits many features in common with plant senescence [77].

Proteolysis is catalyzed by proteases whose activity is regulated mainly by specific plant protease inhibitors both detected by transcriptomics and/or proteomics [76]. The latter are important, not only for inhibiting proteases activated on drought, but also for osmoprotection, since many of them are highly hydrophilic. The striking diversity of plant proteases and of their inhibitors in each species [76] coupled with the fact that very few of their natural substrates are known [78], complicates research in this field. In addition, it appears that the changes in abundance of many proteases in plants stressed by drought have not been detected by

proteomics, due to their low abundance. A combination of proteome analysis and measurement of activities is therefore needed. The proteases most often reported to be involved in the response to drought are cysteine endopeptidases [79, 80], although research on legume plants has indicated participation of other catalytic types of protease, such as serine and aspartic endopeptidases [81, 82].

The response to drought at the level of leaf proteases has been relatively extensively investigated in common bean. Different types of protease have been studied at levels ranging from gene expression to proteolytic activity. In several cases, cultivars with different sensitivities to water deficit have been investigated and changes in proteolytic activity correlated with cultivar sensitivity [46, 54, 82]. In leaf extracts from Brazilian cultivars several endoproteolytic activities with different pH optima were higher in plants under drought. This effect correlated with the level of sensitivity to drought of cultivars [54, 82]. Our research, carried out on cultivars of European origin differing in sensitivity, showed the involvement in response to this stress of different classes of endopeptidases [46]. Increased activities with pH optima in the acid region were observed in leaf extracts of the more sensitive cultivars and were assigned to cysteine and serine proteases. It should be emphasized that differential analysis of leaf proteomes indicated higher abundances of cysteine proteinase precursors in stressed samples [15]. In addition, we have found that the activities of five aminopeptidases in leaves of common bean changed when plants were subjected to drought, this response depending on the developmental stage of the leaves [83].

We have further isolated and characterized, at the protein and gene levels, a protease from the leaves of a common bean that is influenced by drought [81]. It has been classified as a new plant subtilisin-like serine protease. While its gene expression did not change on water deficit, its proteolytic activity did. Further, in common bean leaves an aspartic protease was characterized whose activity was strongly induced on water deficit [82, 84]. It was shown that proteolytic processing of its precursor form was induced by drought, and this, together with the effect of stress on the level of its transcript, led to the suggestion that water deficit regulates activity at both the transcriptional and PTM levels. This response occurs earlier and is stronger in the cultivar more susceptible to drought.

5. Applications of QTL and molecular markers in breeding for drought tolerance

5.1 QTL mapping

Quantitative trait locus (QTL) mapping is an established approach for detecting loci associated with complex quantitative traits, such as, plant tolerance to drought. In common bean multiple populations derived from crosses of susceptible and tolerant parental genotypes, belonging to either a single gene pool, or both Andean and Mesoamerican gene-pools, have been genotyped and genetic linkage maps constructed [18, 85]. Their precision and resolution have been greatly improved by novel sequencing technology and genetic markers, such as, SNPs. For instance, two inter-gene pool populations of 'BAT93' × 'JaloEEP558' and 'DOR364' × 'G19833' have been genotyped repeatedly using a variety of marker systems, ranging from SSR and amplified fragment length polymorphism (AFLP) to SNP [18, 85]. The efforts have culminated in consensus linkage map generation joining both major inter-gene pool maps as well as serving as a core for integration with Mesoamerican linkage map [18]. These approaches have enabled identification of numerous QTLs, controlling resistance to various viral, bacterial and fungal pathogens as well as multigenic traits such as tolerance to drought, biomass production, yield partitioning, and micronutrient accumulation [86, 87].

Drought response-associated QTLs in common bean have been reported in association with yield, phenology, canopy biomass and biomass partitioning. A Mesoamerican and Andean inter-gene pool genetic map with high marker coverage was utilized to detect phenological and seed weight QTLs associated with drought tolerance [88], while intra-gene pool Mesoamerican mapping population has been utilized to identify drought-associated QTL for phenological and yield-related traits [89] as well as QTL for photosynthate acquisition, accumulation and remobilization traits in drought stress [90].

The translation of reported QTLs into practical use has, however, been limited, due to highly variable common bean germplasm and strong influence of the environmental conditions on the presence of minor QTLs. It would be ideal to perform the validation of the QTL in crop production areas. Establishing controlled and uniform growth conditions for evaluation of a large recombinant inbred line (RIL) population, exceeding hundred genotypes, can however prove difficult and not very practical, so a compromise approach for validation of major QTL could consist of testing a subsample of the most diverse RILs for a selected segregation trait in multiple trials sites [5]. Much of the work in QTL mapping and development of drought-tolerant cultivars has been performed based on the traits of the drought resistance sources of Mesoamerican origin, such as those belonging to the race Durango [5].

5.2 Marker-assisted selection and breeding for drought tolerance

For decades DNA markers have been the most widely used molecular markers in crop improvement, due to their abundance and polymorphisms. Marker-assisted selection enables precise and effective selection of common bean genotypes with specific traits and can greatly facilitate the selection process in breeding [91, 92]. These markers are potentially very useful in trait selection and breeding applications, and have been utilized in our procedures, to offer additional informative value on the common bean genotypes included in the breeding program (not published). The advantage of such an approach is that a broad range of economically important traits can be covered, including disease resistance, abiotic stress tolerance, high yield, earliness, phosphorus uptake, and root morphology. However, the practical utilization of molecular markers is at the beginning, also due to lacking validation across the genotypes of the diverse common bean germplasm.

The marker-assisted selection is especially effective in selection for simple and single gene traits, and has been applied for selection for resistance genes for various common bean diseases of viral, bacterial and fungal origin [93, 94]. Selection for quantitative traits such as quantitative resistance or drought tolerance presents a great challenge as it can involve multiple major and minor QTLs controlling the trait [91]. Improved understanding of the complex drought response mechanisms on the level of physiology and molecular biology has enabled identification of potential molecular markers, which could help us distinguish between drought resistant and susceptible genotypes. Among the recently reported markers associated with the drought response in common bean are AQPs whose expression is discussed in the present chapter under Section 4.1. On the other hand several potentially useful molecular markers associated with drought response traits, such as high yield under drought, have been identified using QTL mapping in a segregating RIL populations [89, 90, 95].

Common strategy of common bean breeding programs for resistance to drought is selection of best yielding genotypes that are cultivated in drought-exposed conditions [37, 41]. In addition to that application of novel breeding approaches

not frequently used in common bean breeding has been described [5]. Recurrent selection has been utilized for breeding for drought resistance in genotypes within the same gene-pool, following a process of pre-breeding in which multiple potential parental genotypes with drought resistance traits are created [40]. Another breeding method, advanced backcrossing, could be potentially useful for simultaneous transfer of multiple genes for improving drought resistance traits across genepools [5]. These breeding approaches could greatly benefit with the future developments in the research of plant drought response mechanisms and discovery of associated molecular markers.

6. Conclusion

Drought tolerance is gaining importance in the breeding of common bean for higher yields under the changing environmental conditions. Studying drought tolerance is thus important in order to understand the underlying mechanisms and to identify markers that could help distinguish the more tolerant common bean genotypes. A highly diverse common bean germplasm, adapted to various growth and climatic conditions, constitutes a valuable pool of traits including potential drought tolerance traits. On the other hand, the great complexity of the common bean response to drought on physiological and molecular levels presents a great problem for more effective breeding. The challenge for the future will be to integrate the data obtained by various approaches that include screening of the transcriptome, proteome and metabolome, using advanced bioinformatics and systems biology, identifying molecular markers and QTLs and elucidating the underlying pathways.

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Conflict of interest

The authors declare no conflict of interest.

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