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Review

Models of osmotic stress as a tool for proteomics and metabolomics of legume seeds

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ABSTRACT

Drought poses a significant challenge to the sustainable development of modern agriculture and to the achievement of high crop yields. Water deficit causes osmotic stress and triggers plant physiological responses characterized by reduced water potential, diminished stomatal conductance, and decreased photosynthetic efficiency. Long-term adaptation to osmotic stress entails intricate metabolic rearrangements, leading to the accumulation of osmoprotectants, activation of antioxidant systems, and increased biosyntheses of stress-protective proteins. The severity and duration of drought, along with plant genotype and developmental stage, influence the plant response to stress, consequently affecting crop yield and quality. Particularly in the context of legumes, which are crucial for human and animal nutrition, understanding adaptive strategies to water deficit is essential for the cultivation of drought-resistant genotypes, primarily because these crops predominantly thrive in semi-arid regions. Proteomics and metabolomics approaches, in turn, serve as valuable tools, offering critical insights into the molecular dynamics governing plant responses to drought stress. Furthermore, the use of reliable drought simulation models is imperative for the effective evaluation of legume response to water scarcity, aiding the cultivation of drought-tolerant varieties. This review highlights the perspectives of utilizing different osmotic stress models to investigate proteome and metabolome alteration within seeds of food legumes.

Keywords: proteomics; metabolomics; osmotic stress; drought; legumes.

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Обзор

Модели осмотического стресса как инструмент для протеомного и метаболомного анализа семян бобовых

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АННОТАЦИЯ

Засуха представляет серьезную проблему для устойчивого развития современного сельского хозяйства и достижения высокой продуктивности сельскохозяйственных культур. Дефицит влаги вызывает осмотический стресс и запускает физиологические реакции растений, которые характеризуются снижением водного потенциала, уменьшением устьичной проводимости и понижением эффективности фотосинтеза. Длительная адаптация к осмотическому стрессу сопровождается сложными метаболическими перестройками, приводящими к накоплению осмопротекторов, активации антиоксидантных систем и усилению биосинтеза стресс-протекторных белков. Степень и продолжительность засухи, наряду с генотипом и стадией развития растений, влияют на реакцию растений на стресс, что, в свою очередь, сказывается на количестве и качестве урожая. В частности, для бобовых, которые играют важнейшую роль в системе питания человека и животных, понимание адаптивных стратегий против засухи имеет большое значение для выведения засухоустойчивых сортов, поскольку эти культуры произрастают преимущественно в полузасушливых регионах. В свою очередь, методы протеомики и метаболомики служат ценными инструментами, позволяющими всесторонне оценивать молекулярную динамику, которая определяет реакцию растений на засуху. Кроме того, для эффективной оценки реакции бобовых на дефицит влаги необходимо использование надежных моделей, имитирующих засуху. В данном обзоре рассматриваются перспективы использования различных моделей осмотического стресса для изучения протеомных и метаболомных изменений в семенах бобовых культур.

Ключевые слова: протеомика; метаболомика; осмотический стресс; засуха; бобовые.

Как цитировать

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ЭКО • ВЕКТОР

BACKGROUND

Abiotic stress exerts a profound influence on agricultural crop productivity worldwide, resulting in substantial yield reductions. The Intergovernmental Panel on Climate Change has emphasized the threat posed by extreme temperatures and water scarcity, which detrimentally affect food quantity and quality [1]. Ongoing climate change is manifested in the consistent elevation of global temperatures and an increased frequency of extreme meteorological events, notably prolonged droughts and persistent heatwaves. Predictive climate models indicate a continuation and intensification of these issues across diverse regions [2]. The substantial decrease in plant productivity, driven by high temperatures and water deficits, presents a significant problem for agricultural systems. Consequently, concerted global efforts are essential to address agricultural losses due to abiotic stresses and ensure long-term food security [3].

In the field of plant biology, the impact of drought on crop yield is a subject of extensive research, emphasizing the importance of understanding the intricate mechanisms underlying plant response and adaptation to water scarcity [4]. Diverse effects of drought were observed across various stages of plant growth, influencing crucial processes from seed germination to reproductive development [2]. The ability of plants to regulate osmotic processes, manage water uptake, and optimize nutrient utilization under limited water availability is essential for their survival and productivity.

Moreover, the impact of drought stress is particularly pronounced in legume crops, which play a vital role in global food systems, providing essential nutrients and contributing to sustainable agricultural practices [5]. These crops are primarily cultivated in rain-fed agricultural systems, making them particularly susceptible to the adverse effects of water scarcity, which significantly impacts their grain composition and nutritional quality [6]. Understanding the influence of drought stress on legume plant physiology and seed content is essential for the development of effective strategies to enhance drought tolerance and mitigate yield losses, ensuring the stability of food production systems worldwide.

In this context, advanced technologies such as proteomics and metabolomics play a pivotal role in unraveling the intricate molecular mechanisms underlying plant stress responses [7]. Comprehensive analyses of plant protein and metabolite profiles can help to identify key molecular pathways involved in stress tolerance and adaptation. Moreover, the use of reliable and accurate models that mimic drought conditions is crucial for evaluating plant responses in controlled environments [8]. The appropriate models can provide valuable insights into the impact of water scarcity on various plant species, thereby facilitating the development of new drought-tolerant genotypes and the implementation of effective strategies for sustainable agricultural practices.

This review provides a comprehensive analysis of the extensive effects of drought on both global food security and legume crop production, emphasizing the indispensable role of advanced proteomic and metabolomic techniques. These approaches are essential not only for deciphering the intricate adaptive mechanisms utilized by plants to combat water scarcity but also for assessing the altered characteristics of legume yields affected by drought conditions. Furthermore, the review emphasizes the relevance of diverse drought simulation models in unraveling the intricate dynamics of plant stress responses.

PLANT RESPONSE TO DROUGHT STRESS

Moisture deficit triggers dehydration in plants, subsequently affecting their metabolism, development, and overall morphology. Changes in physiological processes and metabolic pathways during water scarcity slow down or interrupt plant growth, ultimately compromising crop stability. Drought-related losses of crop yield can range from 30% to 90% [9]. The sensitivity of crops to water deficit also depends on the type of agricultural product harvested — taproots, shoots, leaves, fruits, or seeds.

To attain optimal crop yields of high quality, it is crucial to consider not just the duration but also the timing of stress within the plant developmental cycle. Drought stress, in particular, impacts various stages of vegetative growth, starting from seed germination and extending through shoot and root development, influencing all specialized plant organs engaged in these crucial processes [2].

The overall impact of drought can be substantial, affecting various morphological characteristics including plant height, root length, shoot, and root biomass in both fresh and dry weights, leaf count, shoot proliferation, and root surface area [10]. Decreased turgor pressure, resulting from moisture deficit, directly affects leaf count and total leaf area, leading to diminished leaf surface area. Moderate to severe drought conditions have adverse effects on photosynthetic activity, resulting in reduced plant size, decreased leaf surface area, and compromised overall biomass [11] (Figure).

Soil water deficit initiates a series of physiological responses in plants, foremost among them being stomatal closure [12]. Stomatal closure is regulated by the phytohormone abscisic acid (ABA), which reduces transpiration rates and conserves water resources [13]. However, the closure of stomata restricts gas exchange, causing reduced stomatal conductance and ultimately affecting photosynthesis [14]. In addition, ABA not only regulates stomatal closure but also induces the expression of senescence-associated genes in older leaves as a survival strategy.

Drought stress also has a notable impact on the composition of photosynthetic pigments, resulting in an imbalance between chlorophyll and carotenoids, which can detrimentally affect photosynthetic efficiency. This disruption in pigment composition, coupled with the inhibition of cell division, leads to a reduction in photosynthetic activity and growth during

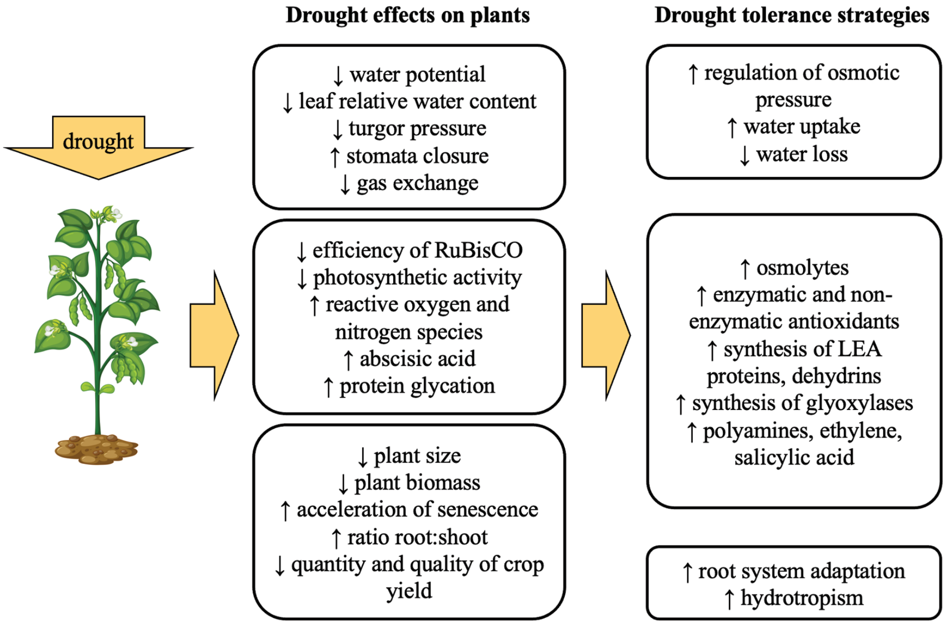

Figure. Impacts of drought on plants and plant strategies for drought tolerance
Рисунок. Воздействие засухи на растения и стратегии устойчивости к ней растений

drought conditions [15]. It is crucial to emphasize that the magnitude of these effects varies among plant species and depends on the developmental stage of the plant [16].

Drought-induced photosynthesis disruption leads to a marked reduction in available resources for plants to allocate toward reproductive processes and floral development. During drought conditions, both the size and abundance of flowers are adversely impacted, along with diminished pollen production and viability. Furthermore, drought can substantially influence the quantity and quality of nectar, thereby altering the dynamics of pollination [17]. These adverse effects on floral characteristics and pollination dynamics have far-reaching implications for plant reproductive success, seed production, and, ultimately, the dynamics of plant populations.

In contrast to the vegetative stage, the reproductive phase of plant growth is notably vulnerable to the detrimental effects of drought. Drought stress during the flowering period and early seed development presents a substantial threat to generative yield, significantly compromising both crop yields and seed quality [18, 19].

Drought during the seed-filling stage can significantly shorten the duration of grain maturation, leading to a substantial reduction in overall crop yields [20]. The water content in storage cells plays a critical role in regulating several physiological mechanisms related to the synthesis and accumulation of essential seed reserves. Notably, the duration of seed filling decreases while the rate of water loss and biomass accumulation increase [21]. Consequently, the quality and nutritional value of seeds, encompassing vital components like proteins, carbohydrates, lipids, minerals, and secondary metabolites, can be predominantly influenced by stress induced by moisture deficit.

The plant response to water deficit varies among species and is influenced by factors such as the plant developmental stage and the environmental conditions [22]. Plants typically employ three key strategies to cope with drought: drought escape, drought avoidance, and drought tolerance [23]. For example, some species escape drought by completing their life cycle before water deficits occur, which is facilitated by rapid development [24]. Drought avoidance involves maintaining relatively high-water content within plant tissues in water-limited conditions by minimizing water loss and optimizing water uptake adequate water supply. For example, crop plants employ root modifications, such as changes in thickness, length, and mass, for efficient water uptake, and reduce transpiration through mechanisms like stomatal closure, leaf curling, and shedding of old leaves [25]. Drought-tolerant plants can grow, flower, and produce viable seeds even under limited resources like water, nutrients, and minerals. Achieving drought tolerance requires a significant energy investment in various drought-tolerance mechanisms [26] (Figure). Different plant species employ diverse drought-protective mechanisms, often using a combination of physiological, morphological, and biochemical adaptations to ensure their survival [27].

Physiological mechanisms encompass increasing water absorption from the soil via the roots, limiting water loss by closing stomata, and regulating osmotic processes within plant tissues [28]. Morphological adaptations help to optimize utilization and minimize losses of water, especially in drought conditions. Indeed, some plants develop deeper and more extensive root systems to access water from deeper soil layers, where water is more abundant [29]. Root systems respond to changes in soil moisture both at the cellular and architectural levels. During water scarcity, roots undergo morphological changes to enhance water and nutrient uptake. This process involves coordinated cell division, elongation, and differentiation in the root apex [30]. In addition, in response to non-homogeneous soil moisture, plants exhibit hydrotropism, where root tips grow towards zones with higher water content. This optimizes root architecture for efficient water acquisition [31].

Biochemical adaptations encompass a diverse array of metabolic and biochemical processes that allow plants to withstand drought stress. These adaptations involve the activation of stress response pathways, including phytohormone signaling, as well as the production and mobilization of antioxidants and specialized osmoprotective metabolites [32].

During osmotic stress, a typical phytohormonal response includes a reduction in endogenous auxins, gibberellins, and cytokinins, alongside an increase in the levels of ABA and ethylene. Dehydration signals stimulate the local production of ABA in various plant organs, which in turn activates specific signaling cascades [33]. In a similar way, ethylene, along with salicylic acid and polyamines, plays crucial roles during osmotic stress. Ethylene, a growth-inhibiting hormone, initiates stress-induced senescence under drought conditions [34]. Polyamines, on the other hand, were observed to influence plant growth and development while also exhibiting free radical scavenging and antioxidant activities [35].

Plants employ a prominent biochemical strategy to improve stress tolerance through metabolic adjustments, leading to increased synthesis of compatible organic solutes known as osmolytes. These osmolytes, including proline, glycine betaine, mannitol, sorbitol, sucrose and other disaccharides, serve crucial roles in protecting plants from stress through various mechanisms. They aid in osmotic regulation, detoxification of reactive oxygen species (ROS), preservation of membrane integrity by maintaining hydrophilic interactions between lipids and proteins, and the upkeep of native protein structures [36]. Among these osmolytes, proline takes center stage due to its high accumulation in leaves under low water potential, a result of both enhanced biosynthesis and reduced mitochondrial oxidation [37]. Glycine betaine, another extensively studied plant osmolyte, interacts with molecules and structures to preserve macromolecule activity, safeguard membrane integrity against stress, and scavenge ROS [38]. Sugars, especially sucrose act as osmolytes as well as important signals in the regulation of stress responses and tolerance mechanisms [39]. It was also shown that abscisic and salicylic acids induce the accumulation of sucrose and enhance drought tolerance [40, 41]. Trehalose is another non-reducing disaccharide, which in addition to its signaling role [42], acts as an osmolyte that stabilizes biological structures under abiotic stress conditions [43]. Furthermore, specific inorganic ions such as Cl^-, Na^+, Ca^{2+}, and K^+ are accumulated as osmolytes in vacuoles and cytosol [44].

In response to the oxidative damages triggered by osmotic stress, which is characterized by the overproduction of ROS, plants employ diverse detoxification mechanisms [45]. These mechanisms encompass enzymatic pathways utilizing enzymes like superoxide dismutase, ascorbate peroxidase, glutathione peroxidase, and catalase, as well as non-enzymatic strategies involving molecules such as ascorbate, glutathione, tocopherol, flavonoids, alkaloids, and carotenoids [46].

At the molecular level, research was focused on the expression of genes directly involved in drought tolerance. Drought induces osmotic and temperature stresses, which can lead to the denaturation of cellular proteins. In response, plants increase the production of specific proteins, including dehydrins, heat shock proteins, and late embryogenesis abundant proteins. These proteins play a vital role in maintaining the integrity of other proteins and preserving normal cell functionality [47, 48]. Additionally, there is an observed increase in the levels of mRNA-binding proteins, antioxidants, enzymes involved in osmolyte biosynthesis, and aquaporin proteins. These components directly or indirectly contribute to the protection of plants under osmotic stress conditions [15].

In conclusion, the study of plant stress response and adaptation strategies is essential for sustainable agriculture. Understanding these mechanisms is key to developing approaches to enhance crop tolerance and address the impacts of climate change.

DROUGHT EFFECTS ON LEGUME CROPS

Legumes play a vital role in human diets worldwide, often serving as a primary source of protein in certain regions [49]. The quality of food legumes is largely determined by their grain composition, which includes essential elements like protein, oil, fatty acids, sugars, dietary fibers, vitamins, and minerals [50].

In addition to their crucial nutritional role, legumes can play a significant role in sustainable agricultural systems [51]. By reducing the usage of nitrogen fertilizers, they contribute to the reduction of greenhouse gas emissions, improve carbon sequestration in soils, and lower fossil energy inputs [52]. Furthermore, legumes are frequently used as intercrops or in crop rotation strategies, offering multiple advantages, including weed control, pest and disease management, and improved farm productivity and income, particularly for smallholder farmers [53, 54].

Grain legume production is confronted with various environmental stresses, with water scarcity being particularly detrimental, causing global yield reductions. Since grain legumes are often grown in rainfed agricultural systems, they are more vulnerable to the adverse effects of drought [6]. To ensure the sustainability and improvement of legume production in the face of climate change, the development of breeding strategies focused on drought-tolerant genotypes is of paramount importance.

The impact of drought stress on grain legume yields is diverse and depends on factors such as phenological stages, soil textures, and agro-climatic regions, leading to variable outcomes among different species [6]. Yield losses attributed to drought were observed in a wide range of grain legumes, including soybean, chickpea, pigeon pea, common bean, cowpea, fava bean, mung bean, and lentil [55]. These losses can fluctuate significantly, typically ranging from 20% to as high as 90% [56]. The magnitude of yield reduction is influenced by several factors, such as the duration and severity of the drought, genetic diversity within the crop, and the developmental stage of the plants [57].

The impact of drought-induced stress extends to rhizobia, leading to morphological changes that can impede infection and nodulation in legumes [58]. Notably, reduced soil moisture conditions led to a significant decline in the number of infection threads in fava beans [59]. Likewise, drought stress caused a reduction in the size of soybean nodules, along with a decrease in the total number of the nodules [60]. Furthermore, the diffusion of oxygen into bacteroids inside the cells of root nodules, as a consequence of drought, disrupts nitrogenase activity, ultimately diminishing symbiotic nitrogen fixation [61]. Consequently, the diminished efficiency of nitrogen metabolism, caused by drought, results in decreased allocation of biomass to reproductive organs [62].

Under water deficit conditions, there is evidence suggesting that grain protein content can rise, as observed in fava bean [63], soybean [64], chickpea [65], and common bean [66]. Conversely, a drought-mediated decline in protein content was demonstrated in chickpea [67], and lupin [68]. These contrasting results are likely influenced by the severity of the drought conditions, genetic diversity within the species, and the specific performance of various legume plants under both field and glasshouse conditions.

Under the influence of drought conditions, alterations in fatty acid composition are significant. Notably, this stress induces an increase in oleic acid content, while simultaneously causing a decrease in the levels of linolenic acid and/or linoleic acid in both peanut and soybean [69, 70]. Particularly during the grain-filling stage, severe drought significantly alters the fatty acid composition in soybean, consequently affecting total oil levels, oil stability, and the overall oil composition [71].

Moreover, the impact of drought stress extends to the starch content of common bean, leading to a decrease. However, it is crucial to note that different behaviors are exhibited between drought-tolerant and sensitive cultivars, particularly concerning grain sucrose contents [72]. In drought-sensitive common bean cultivars, there is a notable decline of 29–47% in sucrose content, whereas in drought-tolerant inbred lines, there might be an increase of up to 43%. In contrast, both lentil and soybean seeds display an augmentation in soluble sugars under drought conditions during the seed-filling stage, indicative of a responsive mechanism to water deficit [73, 74].

The mineral composition of grain legumes might be significantly affected by drought, leading to substantial reductions in various essential elements. In the case of chickpeas, drought induces significant decreases in grain levels of Ca, K, and Na [75]. Likewise, drought-exposed common beans show reductions in grain Fe, Zn, N, and P content [19]. Additionally, lentils manifest notable declines in Zn and Fe concentrations, as well as a decrease in crude protein content under the combined impact of drought and high-temperature conditions [76].

It is crucial to acknowledge that genetic diversity within the same crop species plays a significant role in shaping the metabolite composition and the accumulation of specific metabolites under stress conditions. A notable example is the nuclear magnetic resonance (NMR) analysis conducted on genetically marked pea lines, which unveiled genetic variations linked to specific sets of metabolites present in mature seeds. These variations encompass aromatic amino acids, branched-chain amino acids, metabolites derived from sucrose, secondary metabolites, and several unidentified compounds [77].

Given that drought strongly influences grain mineral composition, protein, and starch contents, fatty acid profile, and antioxidant levels, it is crucial to emphasize the necessity for additional research on the impact of abiotic stresses on legume grain quality. Moreover, the development of programs directed towards enhancing grain quality and improving tolerance to abiotic stresses is imperative [78].

MODELS OF DROUGHT SIMULATION

The challenges posed by drought-induced crop yield losses require the development of new commercially available cultivars with enhanced drought tolerance for economically important agricultural crops. This is imperative to meet the increasing global demand for food [79–81]. However, the creation of drought-tolerant crops depends on a profound understanding of the molecular mechanisms governing plant stress responses and the genetic control of relevant traits at different developmental stages [82]. To effectively investigate plant responses to osmotic stress in controlled conditions, it is crucial to have reliable and suitable stress models. Despite the wide array of available drought models, they can generally be classified into three groups: soil-based, hydroponic, or agar-based. One common characteristic among all these drought stress models is the reduction of water potential in the substrate or medium surrounding the plant roots [8]. Nonetheless, achieving and sustaining precise values of substrate osmotic potential can be demanding. However, the ability to maintain a specific water potential level is pivotal in ensuring the reproducibility and longevity of experiments.

In the case of soil-based models, the osmotic potential of the substrate experiences constant fluctuations as a result of water evaporation from the surface and plant water uptake [83], thereby challenging the reproducibility and predictability of these conditions. Nevertheless, the apparent advantage of this model lies in its representation of authentic drought conditions in both natural settings and agricultural contexts. Notably, these models effectively mimic short-term drought scenarios, frequently encountered in European agricultural practices due to diverse weather conditions [84].

Conversely, hydroponic models rely on a liquid medium and allow a precise evaluation of substrate osmotic potential [85]. From a physical chemistry standpoint, this method involves inducing drought conditions through osmotic stress, achieved by elevating the osmotic pressure of the medium using osmolyte, for example, high-molecular-weight polyethylene glycol (PEG) with an average molecular weight of 6000 Da or higher [86]. However, nutrient solutions containing PEG exhibit high viscosity, potentially impacting root morphology and function [87]. Consequently, compromised root activity can influence leaf dehydration and the overall plant response to stress, which is particularly critical for leguminous crops whose yield directly depends on the efficacy of their symbiosis with rhizobia. Thus, alterations in the plant root structure, nodulation efficiency, or symbiosis stability serve as pivotal indicators of the response to drought conditions [6].

The third approach, known as the agar-based infusion model, stands out as a reliable and user-friendly method for inducing osmotic stress. Consequently, it gained recognition as a versatile tool in physiological experiments involving *Arabidopsis thaliana* seedlings [88]. In contrast to other methods, this model boasts two primary advantages. Firstly, it ensures a stable and reproducible substrate osmotic potential. Secondly, it utilizes a solid substrate that closely emulates authentic soil conditions, thereby minimizing the risk of hypoxia. Consequently, the agar-based model system currently represents an optimal choice for investigating mechanisms related to drought prevention and enhancing drought tolerance [89, 90]. However, its applicability to various crop plant species requires additional validation.

The appropriate and accurate implementation of the experimental osmotic stress model demands a thorough characterization at the physiological, biochemical, and molecular levels. These experiments yield objective insights into the authentic functional state of the plant organism and its metabolic reactions to stress [91]. These data are crucial to verify the stress conditions of experimental plants, specifically the progression of stress responses, and to evaluate the magnitude of alterations induced by stress [8].

All three types of models were proven to be effective for the study of legume crops. For example, a hydroponic system was employed to examine the germination of ten chickpea genotypes under osmotic stress conditions [92]. Similarly, in a separate study, two diverse genotypes of lentils were germinated and cultivated under osmotic stress conditions induced by PEG in a hydroponic system over a 20-day period, with the harvested plant material subsequently used for metabolomics analysis [93]. In addition, the aqueous-based system utilizing PEG infusion has been employed in various studies involving young common bean plants [94, 95]. It is important to note that while the hydroponic system is commonly used for seedlings and young legume plants, our research group successfully applied this model to mature pea plants, inducing osmotic stress during the seed-filling stage [96].

The agar-based PEG-infusion model was effectively optimized for *Arabidopsis thaliana* plants, as evidenced by previous research [88, 89]. Furthermore, this model found application in studies involving various other plants, such as potatoes [97]. In the case of legume plants, the agar-based model was implemented for the performance assessment of young pea plants [91].

The soil-based model, primarily entailing irrigation withholding, remains the most prevalent choice for conducting legume studies. It was employed across various legume species and developmental stages [55], notably serving as a prominent method for investigating legume responses to drought, particularly during the critical stage of seed filling [78]. Furthermore, the application of a PEG solution to the soil substrate can be utilized to induce osmotic stress, as seen in studies involving soybeans, peanuts, and lentils [98–100]. However, one notable limitation of this approach is the potential difficulty in completely removing PEG from the substrate, thereby restricting further plant growth post-drought application.

In conclusion, developing drought-tolerant crops requires a comprehensive understanding of plant stress responses. Various models offer insights into plant reactions to osmotic stress. These models were proven effective in legume studies, contributing to our understanding of their response mechanisms under stress.

APPLICATION OF METABOLOMICS AND PROTEOMICS APPROACHES TO STUDY PLANT RESPONSE TO DROUGHT

To cultivate superior legume varieties with improved stress tolerance, it is imperative to understand the mechanisms governing stress responses. These mechanisms encompass alterations in gene expression, subsequently leading to variations in the transcriptome, proteome, and metabolome [101]. The reliance of breeding programs on quantitative trait loci, candidate genes, and alleles highlighted that genetic variations at the structural and expression levels do not consistently align with the expected phenotype. Furthermore, the intricate nature of stress tolerance mechanisms involves various factors, including the synthesis of metabolites, protein interactions, and post-translational modifications. Hence, these aspects go beyond the limitations of genomics and transcriptomics methodologies [102].

Both proteomics and metabolomics rely on three fundamental approaches: a fractionation method to separate complex mixtures, mass spectrometry (MS) to identify and quantify individual peptides and metabolites, and bioinformatics analyses to correlate the empirical mass data with genomic or metabolite databases. A comprehensive overview of the recent progress in MS-based proteomics and metabolomics techniques was previously provided [7].

Proteomics encompasses a versatile array of techniques utilized for profiling the complex set of expressed proteins within a whole organism, organ, tissue, or cell type. Considering the diverse nature of plant proteins in terms of dynamic range, modifications, molecular weight, charge, hydrophobicity, and cellular distribution, any individual protein isolation protocol inherently incorporates biases toward specific classes of proteins, particularly in whole body or organ extracts [7]. To mitigate these biases, frequently focus on specific tissues, cell types, or subcellular structures during sample preparation [103].

In addition to MS-based techniques for exploring quantitative and qualitative changes in protein expressions, proteomics utilizes diverse methodologies such as NMR, crystallization, electron microscopy, and X-ray diffraction of protein crystals, all aimed at enhancing the understanding of protein structure [104]. Techniques like yeast-two-hybrid assays and protein microarray profiling are also valuable tools for determining protein functions.

The majority of studies dedicated to understanding the plant drought response were primarily focused on the proteomics of green tissues. For instance, research examining the proteomic response of two distinct drought-tolerant maize varieties highlighted the significance of proteins associated with photosystem II repair, photoprotection, electron transport chain, and redox homeostasis in protecting plants against drought stress [105]. Similarly, in legume plants, a comparative analysis of drought-sensitive and drought-tolerant soybean genotypes during the vegetative stage revealed the characteristic up-regulation of several photosynthetic proteins and oxidative stress defence proteins in the drought-tolerant genotype [106]. Another study focusing on the proteomic response of chickpea roots under drought conditions showcased the up-regulation of proteins involved in ROS metabolism, as well as the influence on key proteins related to carbon, energy, secondary metabolism, and signaling pathways [107]. Notably, while the latter study utilized a hydroponic system with the addition of PEG, others employed a soil-based model with water withholding.

Additionally, it is important to highlight the limited focus of studies on drought-induced proteomic changes within seeds. Nonetheless, proteomics analysis of mid-mature peanut seeds grown under water-deficit stress conditions showed the alteration of proteins involved in glycolysis, sucrose and starch metabolism, and fatty acid metabolism [108]. These observed proteomic changes were accompanied by corresponding physiological alterations, including reductions in pod yield and biomass, decreased germination, lowered vigor, compromised seed membrane integrity, increases in storage proteins, and reductions in total fatty acid content. In a recent study, shotgun proteomics of quinoa seeds unveiled the upregulation of chitinase-related proteins under rainfed conditions, which hold potential as biomarkers of drought stress [109].

Metabolomics refers to a comprehensive study of the broad range of metabolites participating in various cellular processes within a biological system [104]. Assessing the relative and absolute levels of metabolites can be achieved through targeted or untargeted analyses. The analytical methods commonly employed for metabolomics largely involve a combination of various MS-based approaches with liquid or gas chromatography techniques, alongside an NMR approach [110, 111].

Metabolomics provides critical insights into the metabolic regulation of developmental and adaptive processes, including protein expression and identifies crucial biochemical processes influencing gene functionality under stress conditions. For instance, in the study of PEG-stimulated osmotic stress using the hydroponic system with two contrasting lentil genotypes, researchers highlighted the differential accumulation of a series of compounds. Particularly, the varying accumulation of specific metabolites, including D-fructose, α, α-trehalose, myo-inositol, and L-tryptophan, in the distinct genotypes, indicated that adaptive metabolic responses to osmotic drought stress operate under strong genotypic dependency [93]. Similarly, the study of drought response in peanut plants grown in a soil-based model also revealed significant differences in the accumulation of metabolites by genotype, with specific metabolites showing increases or decreases depending on the genotype [112]. These findings suggest that each genotype likely exhibits distinct metabolic activities under drought stress.

It is essential to note that limited research was conducted on metabolomics studies related to drought-induced changes in seed metabolite content. A comparison of drought-tolerant and sensitive genotypes of common bean during terminal soil-based drought revealed that the metabolites exhibiting increased content are associated with monobactam biosynthesis, flavone and flavonol biosynthesis, pentose phosphate pathway, C5-branched dibasic acid metabolism, cysteine and methionine metabolism, vitamin B_6 metabolism, and flavonoid biosynthesis [113].

CONCLUSION

Drought-induced changes in protein expression and metabolite composition significantly impact crop yield, nutrient content, and overall quality, thereby posing a substantial threat to global food security. The diversity of adaptive mechanisms employed by plants to counteract osmotic stress underscores the complexity of plant physiology and emphasizes the necessity for comprehensive research initiatives. Since a significant gap exists in comprehending the intricacies of seed proteome and metabolome alterations under drought conditions, further dedicated research focusing on the comprehensive analysis of seeds collected from plants subjected to drought is imperative to unravel the mechanisms underlying plant adaptation and survival strategies in challenging environmental scenarios. This comprehensive understanding is imperative for the development of superior legume varieties with enhanced stress tolerance, ensuring stable agricultural systems and global food security.

ADDITIONAL INFORMATION

Authors' contribution. All authors have made a significant contribution to the development of the concept, critical discussion, and preparation of the article, as well as read and approved the final version before its publication). Personal contribution of the authors: T.S. Leonova — the manuscript concept proposal, literature review, writing the main part of the text; T.E. Bilova — discussing the concept and design of the article, writing and editing the final version of the article; A.A. Frolov — discussing the concept and design of the article, supervising the whole work on the article, writing and editing the final version of the article.

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