



Review

Possible roles of basic helix-loop-helix transcription factors in adaptation to drought



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ABSTRACT

Water deficiency decreases plant growth and productivity. Several mechanisms are activated in response to dehydration that allows plants to cope with stress, including factors controlling stomatal aperture and ramified root system development. In addition, ABA metabolism is also implicated in the regulation of drought responses. The basic helix-loop-helix (bHLH) proteins, a large family of conserved transcription factors that regulates many cellular processes in eukaryotic organisms, are also involved in several responses that are important for plants to cope with drought stress. This review discusses distinct mechanisms related to drought-adaptive responses, especially the possible involvement of the bHLH transcription factors such as MUTE, implicated in stomatal development; RD29, an ABA-responsive gene; EGL3 and GL3, involved in thichome and root hair development; and SPT, which play roles in repressing leaf expansion. Transcription factors are potential targets for new strategies to increase the tolerance of cultivars to drought stress. Recognition of gene regulatory networks in crops is challenging, and the manipulation of bHLH genes as well as components that mediate bHLH transcription factor responses in different pathways could be essential to achieve abiotic stress tolerance in plants through genetic manipulation.

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1. Introduction

Environmental stresses affect plant growth leading to a significant reduction in agricultural production. Soil water deficits are the most adverse environmental conditions limiting agricultural productivity worldwide and generally occur when the available water in the soil is reduced or when atmospheric conditions cause continuous water loss through transpiration or evaporation [1]. Studies using molecular genetics, physiological approaches and gene expression analysis have been performed to elucidate the mechanisms of plant response to water stress [2]. The breeding of crops with introduced abiotic stress tolerance genes has been a sustainable and economically viable solution to address the current alarming climatic situation [3].

Hundreds of water stress responsive genes were identified in *Arabidopsis thaliana* through microarray analyses. Transcription factors were well represented among them, suggesting their importance in the regulation of gene transcription responsive to stress [2]. Great efforts have been exerted to characterize transcription factors involved in stress signaling. Some of the most extensively studied transcription factor families include APETALA2/ethylene-responsive element binding protein (AP2/EREBP), basic leucine zipper (bZIP), *NAM/ATAF1,2/CUC2* (NAC), nuclear factor-Y (NF-Y), zinc finger and basic helix-loop-helix (bHLH) proteins, all of which are highly upregulated in plants subjected to drought stress [4]. We survey current knowledge about a specific group of bHLH transcription factors that may act in signal perception and transduction related to drought stress adaptation. These bHLH transcription factors are listed in Table 1.

The bHLH proteins are members of a large class of transcription factors that are present in all eukaryotic organisms and are involved in a great variety of regulatory processes. These proteins form a monophyletic cluster and constitute the largest transcription factor gene family in plants [5]. This family includes 225 members in *A. thaliana* and 211 in rice [5]. The bHLH transcription factors are characterized by the presence of a highly conserved domain consisting of 50–60 amino acids that form two distinct segments: a stretch of 10–15 basic amino acids (basic region) and a section of approximately 40 amino acids that forms two amphipathic α -helices separated by a loop of variable length (helix-loop-helix region or HLH) [6] (Fig. 1). The HLH domain facilitates protein–protein interactions, enabling the formation of homodimeric or heterodimeric complexes [6]. A large group of plant bHLH proteins contains a basic region that allows them to recognize the E-Box (5'-CANNTG-3') and/or G-Box (5'-CACGTG-3') in the promoter sequences of target genes. Two amino acid residues (Glu-13 and Arg-16) are essential in E-box-binding recognition, which were identified in 359 plant bHLH proteins in an analysis including *Arabidopsis*, poplar, rice, moss and algae [6]. Seven additional bHLH proteins present the Arg-16Lys change without interference in the E-box binding activity. Three additional residues at the basic region (His/Lys-9, Glu-13 and Arg-17) provide DNA binding specificity for the G-box. The G-box recognition motif is lacking in 86 of the 366 E-box DNA binding bHLH, and present in the 280 remained proteins, which are classified as G-box DNA binders. Other bHLHs having more than five basic amino acids at the basic region, but lacking residues, which are essential for the E-box binding recognition specificities are known as non E-box binders. In addition, there are plant bHLH proteins that not present a basic region and are predicted as non DNA binders [6].

The bHLH transcription factors are involved in several processes that are important for plants to cope with drought stress, such as stomatal development [7], root hair formation [8] and the regulation of hormone metabolism [9]. The plant responses to drought stress and the bHLH proteins related to these processes are summarized in Fig. 2.

Much research has been conducted to obtain transgenic drought-resistant plants. These studies have been mainly focused on variations that modify plant growth, producing changes in parameters such as leaf area and stomatal conductance, thereby decreasing water loss and causing the “resistant plants” wilt later than wild type plants. However, these alterations may decrease productivity in the field. Therefore, further experiments are necessary to demonstrate the viability of these transgenic plants in the environment [10].

Transgenic plants have been obtained by different methods and challenged under unfavorable growth conditions to identify good candidate genes for crop breeding. Potato transgenic plants generated by the silencing of *CAP-BINDING PROTEIN 80* gene using artificial microRNA presented higher water deficit tolerance compared with the wild type. These plants presented an increased stomata and trichome densities as well as stomatal closure, when exposed to increased ABA concentration [3].

Transcription factors that regulate networks of stress-responsive genes have often been manipulated in plants to achieve a broader response to a variety of stresses. Rice plants that overexpress dehydration responsive element binding/C-repeat/DRE-binding factor (DREB1/CBF) transcription factors have enhanced tolerance to drought, high salinity or cold stress, as reviewed [11]. Thorough characterization of drought stress-related transcription factors may provide powerful tools for developing crop varieties that have high quality and yields, even when exposed to adverse growth conditions. Drought tolerance could also be used to expand cultivated areas worldwide.

Examples of the genetic manipulation of bHLH transcription factors to improve stress responses in plants were also described. The overexpression of *bHLH122* gene produced *Arabidopsis* transgenic plants more resistant to drought, salt and osmotic stresses. On the other hand, the *bhlh122* loss-of-function mutant was more sensitive to the stresses than wild type plants. The leaves of transgenic plants remained turgid and green with reduced water loss. These transgenic plants showed an efficient stomatal closure reducing transpiration compared to wild type after dehydration. In addition, *bHLH122* directly regulated expression of genes stress related suggesting that this gene is a positive regulator of drought and other stress signaling [12]. Therefore, *bHLH* genes as well as bHLH up/down-stream genes could be good candidates for genetically manipulating plants to achieve abiotic stress tolerance. *CAMTA* gene, a bHLH up-stream gene, constitutes a good candidate for crop improvement due to its role in the regulation of stress related genes expression either in leaf tissue or in root. *CAMTA1* possibly regulates *RD22* gene expression, a bHLH transcription factor, which acts in protecting cells under drought. *camta1* mutant showed growth retardation, poor use water efficiency, high drought sensibility and reduced survivability. The ABA response of *CAMTA1* induced lateral root formation increasing water uptake helping acclimatize and survival of the plant. *CAMTA1* acts as positive regulator of plant growth under drought in *A. thaliana* [13].

The goal of this review is to discuss distinct mechanisms related to drought-adaptive responses, emphasizing the involvement of the *bHLH* genes in these processes and, hence, proposing a detailed assessment of these mutants under abiotic stresses. The mechanisms addressed here are divided into the following four categories: stomatal development; sensitivity to ABA; trichome and root hair development and other protective mechanisms. Genes that control stomata development regulation pathways could modify the stomatal density increasing the use water efficiency; ABA-responsive genes lead to stomatal closure; structures as trichome can reduce the absorption of solar radiation and higher density of root hairs enhance water and nutrient absorption. Besides, limitation of leaf

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