Review

Current Understanding of bHLH Transcription Factors in Plant Abiotic Stress Tolerance

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Abstract: Named for the characteristic basic helix-loop-helix (bHLH) region in their protein structure, bHLH proteins are a widespread transcription factor class in eukaryotes. bHLHs transcriptionally regulate their target genes by binding to specific positions on their promoters and thereby direct a variety of plant developmental and metabolic processes, such as photomorphogenesis, flowering induction, shade avoidance, and secondary metabolite biosynthesis, which are important for promoting plant tolerance or adaptation to adverse environments. In this review, we discuss the vital roles of bHLHs in plant responses to abiotic stresses, such as drought, salinity, cold, and iron deficiency. We suggest directions for future studies into the roles of bHLH genes in plant and discuss their potential applications in crop breeding.

Keywords: abiotic stress; gene regulation; bHLH; transcription factor; tolerance

1. Introduction

Abiotic stresses are major factors inhibiting crop production and reducing crop yields worldwide [1]. These stresses, including extreme temperatures (heat, chilling, and freezing), extreme water levels (flooding and drought), heavy metals, high pH, and salinity [2–4], influence vital biological factors in plants, such as nutrient supply, material biosynthesis, metabolism, and energy supply. If a plant cannot acclimate to abiotic factors that exceed a threshold level, it will experience stress; therefore, to ensure survival in the given conditions, plants employ many acclimatization mechanisms. Different signaling pathways can make plants more tolerant of stresses and allow them to continue to grow under stress conditions; however, the challenge facing researchers is to decipher how the signaling pathways in a specific plant species will acclimate to a given environmental stress.

The stress responses and tolerance levels of plants are inseparable from their expression of specific sets of genes. The basic helix-loop-helix (bHLH) transcription factors (TFs) play important roles in the stress tolerance of plants, in addition to their important roles in reproduction, such as in flower and fruit development [5], and in the biosynthesis of secondary metabolites, such as anthocyanin [6]. However, most reports on bHLH TFs focus on a small subset of model and crop plants. Although a variety of molecular biological methods have been used to explore the roles of bHLH TFs at various stages of plant growth and development and in metabolic pathways and stress responses, much remains to be learned about the functions and regulatory roles of these intriguing proteins. Here, we focus on recent studies of the roles of bHLHs in the molecular mechanisms that regulate abiotic stress tolerance in plants. These studies lay the foundation for improving the stress tolerance of crops.
2. Plant bHLH Genes

The bHLH family is the second largest family of eukaryotic TFs after the MYBs and is widely found in plants. The first plant bHLH gene to be reported was identified in maize (Zea mays L.), and 162 bHLH genes have been identified in the model plant Arabidopsis thaliana (L.) Heynh. [7]. Various bHLH gene numbers have been reported in different plant species; for example, 122 bHLH genes have been identified in pepper (Capsicum annuum L.), which were categorized into 21 subfamilies based on their position-specific conserved amino acids and the presence of other conserved structural domains [8]. In rice (Oryza sativa L.), 167 bHLH family members were identified and classified into 22 subfamilies [9]. In potato (Solanum tuberosum L.), 124 bHLH genes were identified during a whole-genome analysis [10], while in cucumber (Cucumis sativus L.), 142 bHLH genes were identified and classified into 32 subfamilies [11]. In the common bean (Phaseolus vulgaris L.), 155 bHLH genes were identified and classified into 21 subfamilies [12].

The functions of bHLH genes have been analyzed in various biological processes in a variety of flowering plants; for example, 261 bHLH genes were identified in the peanut (Arachis hypogaea L.) genome, and they were assessed for their involvement in pod development [13]. A total of 137 bHLH genes in 26 subfamilies were identified in Jilin ginseng (Panax ginseng C. A. Mey.), some of which were found to function in the saline stress response [14]. In pear (Pyrus bretschneideri Rehder), 197 bHLH genes were identified (classified into 21 groups), with most playing essential roles in stress tolerance [15]. In addition, several other Rosaceae species were analyzed, including peach (Prunus persica (L.) Batsch), apple (Malus × domestica Borkh.), Chinese plum (Prunus mume Siebold & Zucc.), and strawberry (Fragaria vesca L.), for which 129, 188, 122, and 112 bHLH genes were identified, respectively, with many found to function in the stress responses of these plants [16]. Many of the bHLH genes detected in major crops such as rice, wheat (Triticum aestivum L.), and maize were shown to be involved in the responses to abiotic stresses [17]. In Brassica napus L., 460 bHLH genes were identified, which display different expression patterns between different organs, such as the roots and leaves, which may be related to the subfunctionalization of genes [18]. Although these studies represent a good foundation for understanding the roles of bHLHs in plants, the biological and regulatory functions of most of these TFs require further detailed study.

3. Roles of bHLHs in Plant Growth and Development

bHLH TFs participate in many growth and development processes, including seed germination and the development of carpels, anthers, epidermal cells, stomata, and fruit [19]. The Arabidopsis bHLH PHYTOCHROME-INTERACTING FACTOR 1 (PIF1) is a regulator of chlorophyll biosynthesis, which inhibits seed germination in the dark. Light induces the degradation of PIF1 and thus promotes photomorphogenesis [20]. PIF1 degradation is related to phyB activity [21]. In wounded poplar (Populus deltoids) plants, the biosynthesis of anthocyanin, a pigment important in plant defense, is induced via a pathway regulated by PdTT8 (a bHLH transcription factor) together with PdMYB118 (a MYB transcription factor) [22]. Additionally, bHLH TFs play important roles in anthocyanin accumulation in Arabidopsis, which is associated with the jasmonate (JA)-regulated plant defense pathway [23]. CRYPTOCHROME-INTERACTING BASIC HELIX-LOOP-HELIX 1 (CIB1) functions, together with the cryptochromes (CRYs), to promote flower initiation and development by stimulating the expression of flowering locus genes [24,25]. This is the first example of a heterodimeric action by the plant bHLH TFs that alters their DNA-binding affinity or specificity. Subsequently, other types of CIBs were found to jointly regulate the flowering time of Arabidopsis by activating the FLOWERING LOCUS T (FT) promoter and positively regulating the CRY2-mediated flowering pathway [26]. Additionally, bHLH TFs function in the regulation of plant cell elongation during the process of shade avoidance [27].
4. Roles of Plant bHLHs in Biosynthetic Processes

In addition to their roles in growth and development, bHLH TFs play vital roles in plant biosynthetic processes, such as anthocyanin biosynthesis. In peony (Paeonia suffruticosa Andrews) for example, anthocyanin biosynthesis in the flowers is positively regulated by PsbHLH1, which can directly bind to the promoters of dihydroflavonol 4-reductase (PsDFR) and anthocyanidin synthase (PsANS) genes to transcriptionally activate their expression, and could therefore be expected to be used to breed novel color cultivars [28]. In mulberry (Morus alba L.), bHLH3 is a key gene in the regulation of fruit color formation; the pigment composition of mulberry fruits is disrupted by the altered expression of bHLH3 [29]. By contrast, the transgenic expression of the wintersweet (Chimonanthus praecox L.) gene CpbHLH1 inhibits the accumulation of anthocyanin in Arabidopsis [6]. Additionally, members of the bHLH family participate in terpenoid biosynthesis in Medicago truncatula (Gaertn.); the enhanced expression of TRITERPENE SAPONIN BIOSYNTHESIS-ACTivating REGULATOR 1 (TSAR1) and TSAR2 (two JA-induced bHLH genes), together with the upregulation of downstream biosynthetic genes, results in an elevated triterpene saponin content [30]. The carbohydrate and malate accumulation in apples is regulated by the bHLH MdbHLH3 [31]. In Artemisia annua (L.), artemisinin biosynthesis is positively regulated by AabHLH1 [32]. Amygdalin biosynthesis is also regulated by bHLH TFs in almond (Prunus dulcis Miller (D. A. Webb), syn. Prunus amygdalus L.) [33]. Biosynthetic functions for more bHLH genes will likely be identified [34].

5. Roles of bHLH TFs in Plant Stress Tolerance

In addition to the roles of the bHLHs in normal plant growth, development [35], flowering [36], and metabolic biosynthesis [28], many bHLHs function in signal transduction and the response to biotic or abiotic stresses, such as salinity, drought, low temperature, and nutrient deficits [37].

5.1. Roles of bHLH in Drought Tolerance

Drought is a major abiotic stress that limits plant growth and survival, crop quality, and production. bHLH genes respond to drought stress and enhance plant tolerance to water limitation; for example, MdbHLH130 in apple improves the water deficit stress tolerance of transgenic tobacco (Nicotiana tabacum L. “NC89”) by maintaining reactive oxygen species (ROS) homeostasis and inducing stomatal closure [38]. The transgenic expression of PebHLH35 from desert poplar (Populus euphratica Olivier) in Arabidopsis increases tolerance to water deficit stress by regulating stomatal development and photosynthesis in the resulting plants [39]. A genomic analysis in foxtail millet (Setaria italica (L.) P. Beauv.) indicates that many bHLH genes function in drought tolerance [40].

The bHLH-induced enhancement of plant drought tolerance is generally related to abscisic acid (ABA) signaling; for example, bHLH122, which is highly expressed in guard cells, could enhance drought stress tolerance in Arabidopsis by repressing the catabolism of ABA, thus increasing the ABA content [41]. In wheat, drought adaptability is improved by the regulation of the ABA pathway by the TabHLH1 gene [42]. Similarly, drought and ABA treatments increase the expression of PebHLH35 in desert poplar, indicating that this gene is involved in the ABA pathway [39]. In rice, the over-expression of OsbHLH148, which regulates the JA pathway and the function of the OsJAZ (jasmonate ZIM domain) protein, increases the drought tolerance of the plants [43,44]. The ability of water retention and drought tolerance in transgenic Arabidopsis is increased with the expression of MfbHLH38 from the resurrection plant (Myrothamnus flabellifolius Welw.), as well as the increase of their osmotic regulatory ability and oxidative stress tolerance, which is associated with the elevated ABA content and ABA response [45]. A similar result was obtained for the CsbHLH041 gene from cucumber, which enhances the drought tolerance of Arabidopsis and cucumber seedlings [11]. These results indicate that bHLH genes play important roles in plant drought tolerance that associate with phytohormone ABA or JA and ROS scavenging, which highlight new areas of interest for research into crop drought tolerance. Current
studies have focused on hormone-regulated stomatal movement or ROS scavenging, and perhaps, other functions of the bHLH TFs involved in drought stress need to be further explored. A summary model of the roles of bHLHs in plants is displayed in Figure 1.

![Model of the roles of bHLHs in drought tolerance](https://example.com/drought-model.png)

**Figure 1.** Model of the roles of bHLHs in drought tolerance.

### 5.2. Roles of bHLHs in Salt Tolerance

Salinity adversely affects plant growth, reducing germination rates, plant vigor, and crop yields [4,46–48]. In China alone, over one million acres of agricultural soils are contaminated with salt [46,49,50]. Many bHLH genes are involved in plant tolerance to salinity injury and play important roles in improving salt tolerance.

In plants, the first bHLH shown to be involved in salt tolerance, the calcium-binding NaCl-inducible gene 1 (AtNIG1 from Arabidopsis thaliana), was identified in Arabidopsis, with AtNIG1 overexpressors displaying a higher salt tolerance than the corresponding knockout mutants [51]. Similarly, the overexpression of AtbHLH122 confers an increased salt tolerance, osmotic-regulating capacity, and proline concentration [41]. The expression of another bHLH gene, AtbHLH92, is upregulated by salinity and drought [52]. The salt tolerance of Arabidopsis plants was enhanced with the expression of AtMYC2 gene, which is activated by a mitogen-activated protein kinase (MAPK), and is associated with increasing the levels of proline [53]. The functions of bHLH genes have also been explored in non-model plants; for example, CsbHLH041 from cucumber confers ABA-induced salt tolerance in Arabidopsis and cucumber seedlings [11]. The transgenic expression of VvbHLH1 from grape (Vitis vinifera L.) significantly increases flavonoid accumulation and enhances drought tolerance in Arabidopsis [54], while the overexpression of SibHLH22 in tomato (Solanum lycopersicum L.) seedlings improves salt tolerance, enhances ROS scavenging and increases the osmotic adjustment potential [55]. Enhanced salt tolerance was also observed in Arabidopsis heterologously expressing MfbHLH38 from Myrothamnus flabellifolius [45]. Ion transport is an important process in salt tolerance, and some bHLH TFs regulate the Na\(^+/\)H\(^+\) antiporter NHX. For instance, the bHLH TFs AtMYC2 and AtbHLH122 are the upstream regulators of AtNHX1 and AtNHX6, respectively, which enhance salt tolerance in Arabidopsis [56]. Salt tolerance is also enhanced in transgenic Arabidopsis expressing OrbHLH001, a gene from Dongxiang wild rice (Oryza rufipogon Griff.) that is induced by salinity [57], while in cultivated rice, the expression of OsAKT1 (inward-rectifying K\(^+\) channel) is induced and the ionic balance is maintained by the expression of OrbHLH001 under salt stress [58]. Additionally, in maize, ZmbHLH55 improves salt stress tolerance by increasing the accumulation of ascorbic acid through the direct modulation of the expression of genes involved in ascorbic acid biosynthesis [59]. These results provide insights
into the mechanisms by which members of the bHLH gene family respond to salt stress in plants (Figure 2). In fact, certain similarities exist between salt and drought stress; for example, water deficiency stress will be caused, and high ABA levels will be synthesized in plants under either salt or drought stress. While for salt stress, a series of secondary stresses will be caused. Perhaps, the roles of bHLH TFs in maintaining ion homeostasis or metabolic balance in plants under salt stress may be further focused on.

**Figure 2.** Model of the roles of bHLHs in salt tolerance.

5.3. Roles of bHLH in Cold Stress

Low temperature is a major environmental factor that adversely affects plant growth, development, yield, quality, and the geographical distribution of crops. To respond to cold stress, plants must regulate various physiological and biochemical processes, which often requires bHLH TF activity. The transgenic expression of VabHLH1 from the wild amur grape (*Vitis amurensis* Rupr.) enhances the cold tolerance of transgenic Arabidopsis [60], while in rice, OsbHLH1 expression is specifically induced by the cold, indicating that this gene might participate in the cold signaling pathway [61]. Cold tolerance is enhanced in transgenic Arabidopsis plants heterologously expressing two bHLH genes (*ValCE1* (inducer of CBF (C-repeat binding factor) expression) and *ValICE2*) from wild *Vitis amurensis* [62]. The cold tolerance of transgenic pummelo (*Citrus grandis* L. Osbeck) is enhanced by the expression of the trifoliate orange (*Poncirus trifoliata* (L.) Raf.) *PtrbHLH*, gene, which modulates H$_2$O$_2$ levels in plant [63]. In transgenic tobacco, chilling tolerance is enhanced by the expression of *MdClbHLH1* from apple [64]. Furthermore, the transgenic expression of *FibbHLH2* in tartary buckwheat (*Fagopyrum tataricum* (L.) Gaertn.) seedlings is significantly induced by cold stress, and the cold tolerance of transgenic Arabidopsis plants is enhanced by the expression of *FibbHLH2* [65].

As the cold tolerance of trees directly affects their distribution, studying cold tolerance mechanisms could lay the foundation for expanding the range of tree species into colder regions. Several bHLH genes in sweet cherry (*Prunus avium* L.), such as *PavbHLH1*, *PavbHLH18*, *PavbHLH28*, *PavbHLH60*, *PavbHLH61*, *PavbHLH65*, and *PavbHLH66*, are preliminarily shown to be involved in the response to cold stress based on systematic analyses performed on the genome [66]. The bHLH gene *MdbHLH3* enhances the cold tolerance of apples by regulating the increased accumulation of anthocyanin in low temperatures [67]. The transgenic expression of *DICE1* (inducer of CBF expression 1, a bHLH gene) from longan (*Dimocarpus longan* Lour.) enhances the cold tolerance of Arabidopsis by increasing the proline content and reducing the malondialdehyde content in the seedlings [68], which
is similar to the effect in banana [69]. Thus, bHLH genes play important roles in plant cold tolerance that is associated with enhanced proline accumulation, reduced malondialdehyde contents, and reduced electrolyte leakage [70]. Possible regulatory mechanisms involved in bHLH-mediated cold tolerance are shown in Figure 3.

**Figure 3.** Model of the roles of bHLHs in cold stress tolerance.

### 5.4. Roles of bHLH in Iron Deficiency Stress

As a vital micronutrient involved in many metabolic processes, iron is indispensable for plant growth and development [71]. Some bHLH genes have been shown to function in the maintenance of iron homeostasis in plants [72,73]. In Arabidopsis seedlings, AtbHLH105/IAA-LEUCINE RESISTANT 3 (ILR3) is involved in the regulation of iron balance [74], and other bHLH genes, such as AtbHLH38, AtbHLH39, AtbHLH100, AtbHLH101, and AtbHLH115, have been confirmed to play important roles in iron uptake under iron-deficient conditions [75,76]. Other roles of bHLH genes (AtbHLH38 and AtbHLH39) were also identified in Arabidopsis to respond to copper deficiency [77]. In rice, the iron-related transcription factor 3 (OsIR3) that belongs to the bHLH gene family, plays a critical role in maintaining iron homeostasis in an iron-deficient environment [78,79]. In chrysanthemum (chrysanthemum cultivar “Jinba”), iron uptake and H\textsuperscript{+}-ATPase levels are enhanced by the expression of CmbHLH1 in a low-iron environment [80]. Loss-of-function mutant studies reveal that bHLH34 and bHLH104 maintain the iron balance in Arabidopsis, with the mutants displaying a disrupted response to iron deficiency [81,82]. In soybean (*Glycine max* (L.) Merr.), two bHLH genes, *GmbHLH57* and *GmbHLH300*, participate in iron homeostasis under iron-restricted conditions [83]. In tobacco, the expression of *NtbHLH1* is induced under iron deficiency to confer a stress response [84]. In iron-restricted environments, the expression of bHLH genes, such as *AtbHLH29*, is essential for plants to absorb more iron [85]. bHLH genes also play vital roles in responding to iron-deficient conditions and regulating iron uptake and balance in fruit trees, such as pummelo (*Citrus grandis* L.) [86]. These results provide insights that could enable the improvement of iron absorption and utilization in environments with low iron levels (Figure 4). Perhaps, this could provide us a basis for investigating the nutrient balance and elemental utilization, such as nitrogen and calcium, in plants under adversity stress.
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Figure 4. Model of the roles of bHLHs in iron stress tolerance.

Additionally, the functions of various investigated bHLH genes in plants related to abiotic stresses have been summarized and shown in Table 1.

Table 1. Studied basic helix-loop-helix (bHLH) genes that are involved in abiotic stress response in plants.

| Gene          | Function                                                                 | Reference(s) |
|---------------|--------------------------------------------------------------------------|--------------|
| **Drought tolerance** |                                                                          |              |
| MdbHLH130     | Increase water deficit response and reactive oxygen species (ROS)-scavenging ability | [38]         |
| AtbHLH122     | Express in guard cells and increase the abscisic acid (ABA) content       | [41]         |
| TabHLH1       | Be involved in the ABA pathway                                            | [42]         |
| PehHLH35      | Be involved in the ABA pathway                                            | [39]         |
| OsbHLH148     | Be involved in the jasmonate (JA) pathway and increase drought tolerance  | [43]         |
| MfbHLH38      | Increase osmotic regulation and oxidative stress tolerance ability       | [45]         |
| CsbHLH041     | Enhance drought tolerance                                                | [11]         |
| **Salt tolerance** |                                                                          |              |
| AnNIG1        | Bind with calcium and enhance salt tolerance                             | [51]         |
| CsbHLH041     | Be associated with the ABA pathway and enhance salt tolerance            | [11]         |
| AtbHLH122     | Be associated with proline accumulation and enhance salt tolerance       | [41,56]      |
| AtbHLH92      | Response to osmotic stress and enhance salt and drought resistance       | [52]         |
| AtMYC2        | Enhance the proline level and salt tolerance                            | [53]         |
| VcbHLH1       | Be involved in flavonoid accumulation and enhance salt tolerance         | [54]         |
| MfbHLH38      | Be associated with the ABA pathway                                       | [45]         |
| SlbHLH22      | Be associated with ROS scavenging                                        | [55]         |
| OrbHLH001     | Be associated with ionic balance and enhance salt tolerance             | [58]         |
Table 1. Cont.

| Gene          | Function                                                      | Reference(s) |
|---------------|---------------------------------------------------------------|--------------|
| *ZmbHLH55*    | Be involved in ABA biosynthesis and improve salt tolerance   | [59]         |
| **Cold tolerance** |                                                                 |              |
| *VabHLH1*     | Be involved in C-repeat binding factor (CBF) cold signaling pathway and enhance cold tolerance | [60]         |
| *OsbHLH1*     | Participate in the cold signaling pathway                     | [61]         |
| *VaICE1, 2*   | Be involved in the CBF cold signaling pathway                 | [62]         |
| *PtrbHLH*     | Modulate H$_2$O$_2$ levels                                   | [63]         |
| *MdCibHLH1*   | Upregulate *MdCBF2* expression through the CBF pathway       | [64]         |
| *FbHLH2*      | Reduce ROS accumulation and enhance cold tolerance            | [65]         |
| *PavbHLH1, 18, 28, 60, 61, 65, and 66* | Enhance cold tolerance                                        | [66]         |
| *MdbHLH3*     | Be involved in anthocyanin accumulation and enhance cold tolerance | [67]         |
| **Iron homeostasis** |                                                              |              |
| *AtbHLH38, 39, 100, 101, 115* | Regulate iron balance                                       | [74]         |
| *AtbHLH38, 39* | Respond to copper deficiency                                 | [77]         |
| *OsIRO3*      | Maintain iron homeostasis                                    | [79]         |
| *CmbHLH1*     | Regulate iron uptake and H$^+$-ATPase                        | [80]         |
| *AtbHLH34, 104* | Maintain iron balance                                      | [81]         |
| *GmbHLH57, 300* | Participate in iron homeostasis                             | [83]         |
| *NtbHLH1*     | Respond to iron deficiency                                  | [84]         |

6. Summary and Perspectives

The bHLH family of transcription factors has been extensively studied, with increasing attention being paid to their roles as key factors in the responses to environmental stressors, such as low temperatures, salinity, drought, iron or copper deficiency, and even low nitrogen. To date, however, most reports have mainly concentrated on a small subset of model and crop plants. Although some studies have explored the roles of bHLH genes in the growth, development, and stress responses of other plant species using a variety of molecular biological methods, further elucidation of their functions and regulatory roles is still required. Additionally, the roles of bHLH genes in other plants, such as halophytes, should be further explored. This review highlights several directions for future research that will reveal the roles of bHLH genes in plants and facilitate the usage of these genes in crops, particularly in efforts to breed crop varieties with improved stress tolerance, while the regulatory mechanisms of bHLH TFs still need to be investigated systematically.

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References

1. Rosenzweig, C.; Elliott, J.; Deryng, D.; Ruane, A.C.; Müller, C.; Arneth, A.; Boote, K.J.; Folberth, C.; Glotter, M.; Khabarov, N.; et al. Assessing agricultural risks of climate change in the 21st century in a global gridded crop model intercomparison. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 3268–3273. [CrossRef]

2. Suzuki, N.; Rivero, R.M.; Shulaev, V.; Blumwald, E.; Mittler, R. Abiotic and biotic stress combinations. *New Phytol.* **2014**, *203*, 32–43. [CrossRef] [PubMed]

3. Guo, J.; Dong, X.; Han, G.; Wang, B. Salt-enhanced reproductive development of *Suaeda salsa* L. coincided with ion transporter gene upregulation in flowers and increased pollen K⁺ content. *Front. Plant Sci.* **2019**, *10*, 333. [CrossRef] [PubMed]

4. Song, J.; Fan, H.; Zhao, Y.; Jia, Y.; Du, X.; Wang, B. Effect of salinity on germination, seedling emergence, seedling growth and ion accumulation of a euryhaline *Suaeda salsa* in an intertidal zone and on saline inland. *Aquat. Bot.* **2008**, *88*, 331–337. [CrossRef]

5. Sun, W.; Jin, X.; Ma, Z.; Chen, H.; Liu, M. *Basic helix-loop-helix* (bHLH) gene family in Tartary buckwheat (*Fagopyrum tataricum*): Genome-wide identification, phylogeny, evolutionary expansion and expression analyses. *Int. J. Biol. Macromol.* **2020**, *155*, 1478–1490. [CrossRef]

6. Zhao, R.; Song, X.; Yang, N.; Chen, L.; Xiang, L.; Liu, X.Q.; Zhao, K. Expression of the subgroup IIIb bHLH transcription factor *CpbHLH1* from *Chimonanthus praecox* (L.) in transgenic model plants inhibits anthocyanin accumulation. *Plant Cell Rep.* **2020**, *39*, 891–907. [CrossRef] [PubMed]

7. Bailey, P.C.; Martin, C.; Toledo-Ortiz, G.; Quail, P.H.; Huq, E.; Heim, M.A.; Jakoby, M.; Werber, M.; Weisshaar, B. Update on the basic helix-loop-helix transcription factor gene family in *Arabidopsis thaliana*. *Plant Cell* **2003**, *15*, 2497–2502. [CrossRef] [PubMed]

8. Zhang, Z.; Chen, J.; Liang, C.; Liu, F.; Hou, X.; Zou, X. Genome-wide identification and characterization of the bHLH transcription factor family in pepper (*Capsicum annuum* L.). *Front. Genet.* **2020**, *11*, 1156. [CrossRef]

9. Li, X.; Duan, X.; Jiang, H.; Sun, Y.; Tang, Y.; Yuan, Z.; Guo, J.; Liang, W.; Chen, L.; Yin, J.; et al. Genome-wide analysis of basic/helix-loop-helix transcription factor family in rice and *Arabidopsis*. *Plant Physiol.* **2006**, *141*, 1167–1184. [CrossRef]

10. Wang, R.; Zhao, F.; Kong, N.; Lu, R.; Pei, Y.; Huang, C.; Ma, H.; Chen, Q. Genome-wide identification and characterization of the potato bHLH transcription factor family. *Genes* **2018**, *9*, 54. [CrossRef]

11. Li, J.; Wang, T.; Han, J.; Ren, Z. Genome-wide identification and characterization of cucumber bHLH family genes and the functional characterization of *CsbHLH041* in NaCl and ABA tolerance in *Arabidopsis* and cucumber. *BMC Plant Biol.* **2020**, *20*, 272. [CrossRef]

12. Kavas, M.; Baloğlu, M.C.; Atabay, E.S.; Ziplar, U.T.; Ünver, T. Genome-wide characterization and expression analysis of common bean bHLH transcription factors in response to excess salt concentration. *Mo. Genet. Genomic* **2016**, *291*, 129–143. [CrossRef]

13. Gao, C.; Sun, J.; Wang, C.; Dong, Y.; Xiao, S.; Wang, X.; Jiao, Z. Genome-wide analysis of basic/helix-loop-helix gene family in peanut and assessment of its roles in pod development. *PLoS ONE* **2017**, *12*, e0181843. [CrossRef]

14. Zhu, L.; Zhao, M.; Chen, M.; Li, L.; Jiang, Y.; Liu, S.; Jiang, Y.; Wang, K.; Wang, Y.; Sun, C.; et al. The bHLH gene family and its response to saline stress in *Jilin ginseng*, *Panax ginseng* C.A. Meyer. *Mo. Genet. Genomic* **2020**, *295*, 877–890. [CrossRef]

15. Dong, H.; Chen, Q.; Dai, Y.; Hu, W.; Zhang, S.; Huang, X. Genome-wide identification of *PbrbHLH* family genes, and expression analysis in response to drought and cold stresses in pear (*Pyrus bretschneideri*). *BMC Plant Biol.* **2021**, *21*, 86. [CrossRef] [PubMed]

16. Kout, X.; Xiong, C.; Wang, D.; Sun, Y.; Wang, P.; Wu, J.; Zhang, S. Comparative analysis of bHLH transcription factors in five Rosaceae species, and expression analysis of PbbHLHs in response to drought stress in pear. *Res. Sq.* **2020**, *21*, 1023. [CrossRef]

17. Wei, K.; Chen, H. Comparative functional genomics analysis of bHLH gene family in rice, maize and wheat. *BMC Plant Biol.* **2018**, *18*, 309. [CrossRef]

18. Shen, W.; Cui, X.; Li, H.; Teng, R.M.; Wang, Y.X.; Liu, H.; Zhuang, J. Genome-wide identification and analyses of bHLH family genes in *Brassica napus*. *Can. J. Plant Sci.* **2019**, *99*, 589–598. [CrossRef]

19. Groszmann, M.; Bylstra, Y.; Lampugnani, E.R.; Smyth, D.R. Regulation of tissue-specific expression of *Spatula*, a bHLH gene involved in carpel development, seedling germination, and lateral organ growth in *Arabidopsis*. *J. Exp. Bot.* **2010**, *61*, 1495–1508. [CrossRef]

20. Shen, H.; Moon, J.; Huq, E. *PIF1* is regulated by light-mediated degradation through the ubiquitin-26S proteasome pathway to optimize photomorphogenesis of seedlings in *Arabidopsis*. *Plant J.* **2005**, *44*, 1023–1035. [CrossRef]

21. Paik, I.; Chen, F.; Ngoc Pham, V.; Zhu, L.; Kim, J.-I.; Huq, E. A phyB-PIF1-SPA1 kinase regulatory complex promotes photomorphogenesis in *Arabidopsis*. *Nat. Commun.* **2010**, *10*, 4216. [CrossRef]

22. Wang, H.; Wang, X.; Yu, C.; Wang, C.; Jin, Y.; Zhang, H. MYB transcription factor *PdMYB118* directly interacts with bHLH transcription factor *PdTT8* to regulate wound-induced anthocyanin biosynthesis in poplar. *BMC Plant Biol.* **2020**, *20*, 173. [CrossRef] [PubMed]
23. Qi, T.; Song, S.; Ren, Q.; Wu, D.; Huang, H.; Chen, Y.; Fan, M.; Peng, W.; Ren, C.; Xie, D. The Jasmonate-ZIM-domain proteins interact with the WD-Repeat/bHLH/MBY complexes to regulate jasmonate-mediated anthocyanin accumulation and trichome initiation in Arabidopsis thaliana. Plant Cell 2011, 23, 1795–1814. [CrossRef] [PubMed]

24. Liu, H.; Yu, X.; Li, K.; Kleinjot, J.; Yang, H.; Lisiero, D.; Lin, C. Photocrossed CRY2 interacts with CIB1 to regulate transcription and floral initiation in Arabidopsis. Science 2008, 322, 1535–1539. [CrossRef]

25. Liu, H.; Wang, Q.; Liu, Y.; Zhao, X.; Imaizumi, T.; Somers, D.E.; Tobin, E.M.; Lin, C. Arabidopsis CRY2 and ZTL mediate blue-light regulation of the transcription factor CIB1 by distinct mechanisms. Proc. Natl. Acad. Sci. USA 2013, 110, 17582–17587. [CrossRef]

26. Liu, Y.; Li, X.; Li, K.; Liu, H.; Lin, C. Multiple bHLH proteins form heterodimers to mediate CRY2-dependent regulation of flowering-time in Arabidopsis. PLoS Genet. 2013, 9, e1003861. [CrossRef]

27. Buti, S.; Hayes, S.; Pierik, R. The bHLH network underlying plant shade-avoidance. Physiol. Plant 2020, 169, 312–324. [CrossRef]

28. Qi, Y.; Zhou, L.; Han, L.; Zhou, H.; Miao, K.; Wang, Y. PsbHLH1, a novel transcription factor involved in regulating anthocyanin biosynthesis in tree peony (Paeonia suffruticosa). Plant Physiol. Biochem. 2020, 154, 396–408. [CrossRef]

29. Li, H.; Yang, Z.; Zeng, Q.; Wang, S.; Luo, Y.; Huang, Q.; Xin, Y.; He, N. Abnormal expression of bHLH3 disrupts a flavonoid homeostasis network, causing differences in pigment composition among mulberry fruits. Hortic. Res. 2020, 7, 83. [CrossRef]

30. Mertens, J.; Pollier, J.; Vandendriessche, R.; Lopez-Vidriero, I.; Franco-Zorrilla, J.M.; Goossens, A. The bHLH transcription factors TSAR1 and TSAR2 regulate triterpene saponin biosynthesis in Medicago truncatula. Plant Physiol. 2016, 170, 194–210. [CrossRef]

31. Yu, J.Q.; Gu, K.D.; Sun, C.H.; Zhang, Q.Y.; Wang, J.H.; Ma, F.F.; You, C.X.; Hu, D.G.; Hao, Y.J. The apple bHLH transcription factor MdbHLH3 functions in determining the fruit carbohydrates and malate. Plant Biotechnol. J. 2020, 19, 285–299. [CrossRef] [PubMed]

32. Ji, Y.; Xiao, J.; Shen, Y.; Ma, D.; Li, Z.; Pu, G.; Li, X.; Huang, L.; Liu, B.; Ye, H.; et al. Cloning and characterization of AabHLH1, a bHLH transcription factor that positively regulates artemisinin biosynthesis in Artemisia annua. Plant Cell Physiol. 2014, 55, 1592–1604. [CrossRef] [PubMed]

33. Sánchez-Pérez, R.; Pavan, S.; Mazzeo, R.; Moldovan, C.; Cigliano, R.A.; Del Cueto, J.; Müller, B.L. Mutation of a bHLH transcription factor allowed almond domestication. Science 2019, 364, 1095–1098. [CrossRef] [PubMed]

34. Shi, Q.; Li, X.; Du, J.; Li, X. Anthocyanin synthesis and the expression patterns of bHLH transcription factor family during floral initiation in Arabidopsis thaliana. Plant Physiol. Res. Commun. 2014, 450, 453–458. [CrossRef]

35. Pires, N.; Dolan, L. Origin and diversification of basic-helix-loop-helix proteins in plants. Mol. Biol. Evol. 2010, 27, 862–874. [CrossRef]

36. Castelain, M.; Hir, R.L.; Bellini, C. The non-DNA-binding bHLH transcription factor PRE3/bHLH135/ATBS1/TMO7 is involved in the regulation of light signaling pathway in Arabidopsis. Physiol. Plantarum. 2012, 145, 450–460. [CrossRef]

37. Abe, H.; Urao, T.; Ito, T.; Seki, M.; Shinozaki, K.; Yamaguchi-Shinozaki, K. Arabidopsis AtMYC2 (bHLH) and AtMYB2 (MYB) function as transcriptional activators in abscisic acid signaling. Plant Cell 2003, 15, 63–78. [CrossRef]

38. Zhao, Q.; Fan, Z.; Qiu, L.; Che, Q.; Wang, Y. MdbHLH130, an apple bHLH transcription factor, confers water stress resistance by regulating stomatal closure and ROS homeostasis in transgenic tobacco. Front. Plant Sci. 2020, 11, 543696. [CrossRef]

39. Dong, Y.; Wang, C.; Han, X.; Tang, S.; Liu, S.; Xia, X.; Yin, W. A novel bHLH transcription factor PehHLH35 from Populus euphratica confers drought tolerance through regulating stomatal development, photosynthesis and growth in Arabidopsis. Biochem. Biophys. Res. Commun. 2014, 450, 453–458. [CrossRef]

40. Wang, P.; Wang, H.; Wang, Y.; Ren, F.; Liu, W. Analysis of bHLH genes from foxtail millet (Setaria italica) and their potential relevance to drought stress. PLoS ONE 2018, 13, e0207344. [CrossRef]

41. Liu, W.; Tai, H.; Li, S.; Gao, W.; Zhao, M.; Xie, C.; Li, W.X. bHLH122 is important for drought and osmotic stress resistance in Arabidopsis and in the repression of ABA catabolism. New Phytol. 2014, 201, 1192–1204. [CrossRef]

42. Yang, T.; Yao, S.; Hao, L.; Zhao, Y.; Lu, W.; Xiao, K. Wheat bHLH-type transcription factor gene TabHLH1 is crucial in mediating osmotic stresses tolerance through modulating largely the ABA-associated pathway. Plant Cell Rep. 2016, 35, 2309–2323. [CrossRef]

43. See, J.S.; Joo, K.; Kim, M.J.; Kim, Y.K.; Nahm, B.H.; Song, S.I.; Cheong, J.J.; Lee, J.S.; Kim, J.K.; Choi, Y.D. OsbHLH148, a basic-helix-loop-helix protein, interacts with OsJAZ proteins in a jasmonate signaling pathway leading to drought tolerance in rice. Plant J. 2011, 65, 907–921. [CrossRef]

44. Kiribuchi, K.; Sugimori, M.; Takeda, M.; Otani, T.; Okada, K.; Onodera, H.; Ugaki, M.; Tanaka, Y.; Tomiyama-Akimoto, C.; Yamaguchi, T.; et al. RER1, a jasmonic acid-responsive gene from rice, encodes a basic helix-loop-helix protein. Biochem. Biophys. Res. Co. 2004, 325, 857–865. [CrossRef]

45. Qiu, J.R.; Huang, Z.; Xiang, X.Y.; Xu, W.X.; Wang, J.T.; Chen, J.; Song, L.; Xiao, Y.; Li, X.; Ma, J.; et al. MtbHLH38, a Myrothamnus flabellifolia bHLH transcription factor, confers tolerance to drought and salinity stresses in Arabidopsis. BMC Plant Biol. 2020, 20, 542. [CrossRef]

46. Shabala, S. Learning from halophytes: Physiological basis and strategies to improve abiotic stress tolerance in crops. Ann. Bot. 2013, 112, 1209–1221. [CrossRef]

47. Guo, J.; Suo, S.; Wang, B. Sodium chloride improves seed vigour of the euhalophyte Suaeda salsa. Seed Sci. Res. 2015, 25, 335–344. [CrossRef]

48. Liu, R.; Cui, B.; Jia, T.; Song, J. Role of Suaeda salsa SsNRT2.1 in nitrate uptake under low nitrate and high saline conditions. Plant Physiol. Biochem. 2021, 159, 171–178. [CrossRef]
51. Kim, J.; Kim, H.Y. Functional analysis of a calcium-binding transcription factor involved in plant salt stress signaling. FEBS Lett. 2006, 580, 5251–5256. [CrossRef] 

52. Jiang, Y.; Yang, B.; Deyholos, M.K. Functional characterization of the Arabidopsis bHLH92 transcription factor in abiotic stress. Mol. Genet. Genomic 2009, 282, 503–516. [CrossRef] 

53. Verma, D.; Jalmi, S.K.; Bhagat, P.K.; Verma, N.; Sinha, A.K. A bHLH transcription factor, MYC2, imparts salt intolerance by regulating proline biosynthesis in Arabidopsis. Fems J. 2020, 287, 2560–2576. [CrossRef] [PubMed] 

54. Wang, F.; Zhu, H.; Kong, W.; Peng, R.; Liu, Q.; Yao, Q. The Antirrhinum AmDEL gene enhances flavonoid accumulation and salt and drought tolerance in transgenic Arabidopsis. Planta 2016, 244, 59–73. [CrossRef] [PubMed] 

55. Waseem, M.; Rong, X.; Li, Z. Dissecting the role of a basic helix-loop-helix transcription factor, SbHLH22, under salt and drought stresses in transgenic Solanum lycopersicum L. Front. Plant Sci. 2019, 10, 734. [CrossRef] [PubMed] 

56. Krishnamurthy, P.; Vishal, B.; Khoo, K.; Rajappa, S.; Loh, C.S.; Kumar, P. Expression of AoNHX1 increases salt tolerance of rice and Arabidopsis, and bHLH transcription factors regulate AtNHX1 and AtNHX6 in Arabidopsis. Plant Cell Rep. 2019, 38, 1299–1315. [CrossRef] 

57. Li, F.; Guo, S.; Zhao, Y.; Chen, D.; Chong, K.; Xu, Y. Overexpression of a homopeptide repeat-containing bHLH protein gene (OrbHLH001) from Dongxiang Wild Rice confers freezing and salt tolerance in transgenic Arabidopsis. Plant Cell Rep. 2010, 29, 977–986. [CrossRef] 

58. Chen, Y.; Li, F.; Ma, Y.; Chong, K.; Xu, Y. Overexpression of OrbHLH001, a putative helix–loop–helix transcription factor, causes increased expression of AKT1 and maintains ionic balance under salt stress in rice. J. Plant Physiol. 2013, 170, 93–100. [CrossRef] 

59. Yu, C.; Yan, M.; Dong, H.; Luo, J.; Ke, Y.; Guo, A.; Chen, Y.; Zhang, J.; Huang, X. Maize bHLH55 functions positively in salt tolerance through modulation of AsA biosynthesis by directly regulating GDP-mannose pathway genes. Plant Sci. 2021, 302, 110676. [CrossRef] 

60. Xu, W.; Zhang, N.; Jiao, Y.; Li, R.; Xiao, D.; Wang, Z. The grapevine basic helix-loop-helix (bHLH) transcription factor positively modulates CBF-pathway and confers salt tolerance in transgenic Arabidopsis. Mol. Biol. Rep. 2014, 41, 5329–5342. [CrossRef] 

61. Wang, Y.J.; Zhang, Z.G.; He, X.J.; Zhou, H.L.; Wen, Y.X.; Dai, J.X.; Zhang, J.S.; Chen, S.Y. A rice transcription factor OsbHLH1 is involved in cold stress response. Theor. Appl. Genet. 2003, 107, 1402–1409. [CrossRef] 

62. Xu, W.; Jiao, Y.; Li, R.; Zhang, N.; Xiao, D.; Ding, X.; Wang, Z. Chinese wild-growing Vitis amurensis ICE1 and ICE2 encode MYC-type bHLH transcription activators that regulate cold tolerance in Arabidopsis. PLoS ONE 2014, 9, e102303. [CrossRef] 

63. Geng, J.; Wei, T.; Wang, Y.; Huang, X.; Liu, J.H. Overexpression of PtrbHLH, a basic helix-loop-helix transcription factor from Poncirus trifoliata, confers enhanced cold tolerance in pummelo (Citrus grandis) by modulation of H2O2 level via regulating a CAT gene. Tree Physiol. 2019, 39, 2045–2054. [CrossRef] 

64. Feng, X.M.; Zhao, Q.; Zhao, L.L.; Qiao, Y.; Xie, X.B.; Li, H.F.; Yao, Y.X.; You, C.X.; Hao, Y.J. The cold-induced basic helix-loop-helix transcription factor positively modulates CBF pathway and confers cold stress in transgenic Arabidopsis. Mol. Biol. Rep. 2014, 41, 5329–5342. [CrossRef] 

65. Yao, P.; Sun, Z.; Li, C.; Zhao, X.; Li, M.; Deng, R.; Huang, Y.; Zhao, H.; Chen, H.; Wu, Q. Overexpression of Fagopyrum tataricum FtbHLH2 enhances tolerance to cold stress in transgenic Arabidopsis. Plant Physiol. Biochem. 2018, 125, 85–94. [CrossRef] 

66. Shen, T.; Wen, X.; Wen, Z.; Qiu, Z.; Hou, Q.; Li, Z.; Mei, L.; Yu, H.; Qiao, G. Genome-wide identification and expression analysis of bHLH transcription factor family in response to cold stress in sweet cherry (Prunus avium) model. Mol. Genet. Genomic 2015, 287, 503–516. [CrossRef] 

67. Xie, X.B.; Li, S.; Zhang, R.F.; Zhao, J.; Chen, Y.C.; Zhao, Q.; Yao, Y.X.; You, C.X.; Zhang, X.S.; Hao, Y.J. The bHLH transcription factor MdbHLH promotes anthocyanin accumulation and fruit colouration in response to low temperature in apples. Plant Cell Environ. 2012, 35, 1884–1897. [CrossRef] 

68. Yang, X.; Wang, R.; Hu, Q.; Li, S.; Mao, X.; Jing, H.; Zhao, J.; Hu, G.; Fu, J.; Liu, C. DIICE1, a stress-responsive gene from Dimocarpus longan, enhances cold tolerance in transgenic Arabidopsis. Plant Physiol. Biochem. 2019, 142, 490–499. [CrossRef] 

69. Peng, H.H.; Shan, W.; Kuan, J.F.; Lu, W.J.; Chen, J.Y. Molecular characterization of cold-responsive basic helix-loop-helix transcription factors MabHLHs that interact with MalICE in banana fruit. Planta 2013, 238, 937–953. [CrossRef] 

70. Luo, P.; Li, Z.; Chen, W.; Xing, W.; Yang, J.; Cui, Y. Overexpression of RmICE1, a bHLH transcription factor from Rosa multiflora, enhances cold tolerance via modulating ROS levels and activating the expression of stress-responsive genes. Environ. Exp. Bot. 2020, 178, 104160. [CrossRef] 

71. Gao, F.; Robe, K.; Gaymard, F.; Izquierdo, E.; Dubos, C. The transcriptional control of iron homeostasis in plants: A tale of bHLH transcription factors? Front. Plant Sci. 2019, 10, 6. [CrossRef] [PubMed] 

72. Wang, M.; Gong, J.; Bhullar, N.K. Iron deficiency triggered transcriptome changes in bread wheat. Comput. Struct. Biotechnol. J. 2020, 18, 2709–2722. [CrossRef] [PubMed] 

73. Long, T.A.; Tsukagoshi, H.; Busch, W.; Lahner, B.; Salt, D.E.; Benfey, P.N. The bHLH transcription factor POPEYE regulates response to iron deficiency in roots. Plant Cell 2010, 22, 2219–2236. [CrossRef] [PubMed]
74. Tissot, N.; Robe, K.; Gao, F.; Grant-Grant, S.; Boucherez, J.; Bellegarde, F.; Maghiaoui, A.; Marcelin, R.; Izquierdo, E.; Benhamed, M.; et al. Transcriptional integration of the responses to iron availability in Arabidopsis by the bHLH factor ILR3. *New Phytol.* 2019, 223, 1433–1446. [CrossRef] [PubMed]

75. Wang, N.; Cui, Y.; Liu, Y.; Fan, H.; Du, J.; Huang, Z.; Yuan, Y.; Wu, H.; Ling, H.-Q. Requirement and functional redundancy of lb subgroup bHLH proteins for iron deficiency responses and uptake in *Arabidopsis thaliana*. *Mol. Plant* 2013, 6, 503–513. [CrossRef] [PubMed]

76. Liang, G.; Zhang, H.; Li, X.; Ai, Q.; Yu, D. bHLH transcription factor bHLH115 regulates iron homeostasis in *Arabidopsis thaliana*. *J. Exp. Bot.* 2017, 68, 1743–1755. [CrossRef] [PubMed]

77. Cai, Y.; Li, Y.; Liang, G. FIT and bHLH Ib transcription factors modulate iron and copper crosstalk in Arabidopsis. *Plant Cell Environ.* 2021, 44, 1679–1691. [CrossRef]

78. Wang, F.; Itai, R.N.; Nozoye, T.; Kobayashi, T.; Nishizawa, N.K.; Nakanishi, H. The bHLH protein OsIRO3 is critical for plant survival and iron (Fe) homeostasis in rice (*Oryza sativa* L.) under Fe-deficient conditions. *Soil Sci. Plant Nutr.* 2020, 66, 579–592. [CrossRef]

79. Wang, W.; Ye, J.; Ma, Y.; Wang, T.; Shou, H.; Zheng, L. OsIRO3 plays an essential role in iron deficiency responses and regulates iron homeostasis in rice. *Plants* 2020, 9, 1095. [CrossRef]

80. Zhao, M.; Song, A.; Li, P.; Chen, S.; Jiang, J.; Chen, F. A bHLH transcription factor regulates iron intake under Fe deficiency in chrysanthemum. *Sci. Rep.* 2014, 4, 6694. [CrossRef]

81. Li, X.; Zhang, H.; Ai, Q.; Liang, G.; Yu, D. Two bHLH transcription factors, bHLH34 and bHLH104, regulate iron homeostasis in *Arabidopsis thaliana*. *Plant Physiol.* 2016, 170, 2478–2493. [CrossRef]

82. Zhang, J.; Liu, B.; Li, M.; Feng, D.; Jin, H.; Wang, P.; Liu, J.; Xiong, F.; Wang, J.; Wang, H.-B. The bHLH transcription factor bHLH104 interacts with IAA-LEUCINE RESISTANT3 and modulates iron homeostasis in *Arabidopsis*. *Plant Cell* 2015, 27, 787–805. [CrossRef]

83. Li, L.; Gao, W.; Peng, Q.; Zhou, B.; Kong, Q.; Ying, Y.; Shou, H. Two soybean bHLH factors regulate response to iron deficiency. *J. Integr. Plant Biol.* 2018, 60, 608–622. [CrossRef]

84. Li, Y.-Y.; Sui, X.-Y.; Yang, J.-S.; Xiang, X.-H.; Li, Z.-Q.; Wang, Y.-Y.; Zhou, Z.-C.; Hu, R.-S.; Liu, D. A novel bHLH transcription factor, NtbHLH1, modulates iron homeostasis in tobacco (*Nicotiana tabacum* L.). *Biochem. Biophys. Res. Commun.* 2020, 522, 233–239. [CrossRef]

85. Zhang, J.; Zhu, H.-F.; Liang, H.; Liu, F.-K.; Zhang, A.-M.; Ling, H.-Q.; Wang, D.-W. Further analysis of the function of AtBHLH29 in regulating the iron uptake process in *Arabidopsis thaliana*. *J. Integr. Plant Biol.* 2006, 48, 75–84. [CrossRef]

86. Zhang, X.Y.; Qiu, J.Y.; Hui, Q.L.; Xu, Y.Y.; He, Y.Z.; Peng, L.Z.; Fu, X.Z. Systematic analysis of the basic/helix-loop-helix (bHLH) transcription factor family in pummelo (*Citrus grandis*) and identification of the key members involved in the response to iron deficiency. *BMC Genom.* 2020, 21, 233. [CrossRef]