Review

The Role of Transcription Factors in the Regulation of Plant Shoot Branching

Lingling Zhang, Weimin Fang, Fadi Chen * and Aiping Song *

State Key Laboratory of Crop Genetics and Germplasm Enhancement, Key Laboratory of Landscaping, Ministry of Agriculture and Rural Affairs, College of Horticulture, Nanjing Agricultural University, Nanjing 210095, China; 2021204041@stu.njau.edu.cn (L.Z.); fangwm@njau.edu.cn (W.F.)
* Correspondence: chenfd@njau.edu.cn (F.C.); aiping_song@njau.edu.cn (A.S.)

Abstract: Transcription factors, also known as trans-acting factors, balance development and stress responses in plants. Branching plays an important role in plant morphogenesis and is closely related to plant biomass and crop yield. The apical meristem produced during plant embryonic development repeatedly produces the body of the plant, and the final aerial structure is regulated by the branching mode generated by axillary meristem (AM) activities. These branching patterns are regulated by two processes: AM formation and axillary bud growth. In recent years, transcription factors involved in regulating these processes have been identified. In addition, these transcription factors play an important role in various plant hormone pathways and photoreponses regulating plant branching. In this review, we start from the formation and growth of axillary meristems, including the regulation of hormones, light and other internal and external factors, and focus on the transcription factors involved in regulating plant branching and development to provide candidate genes for improving crop architecture through gene editing or directed breeding.

Keywords: transcription factors; branching; axillary meristem; development

1. Introduction

Transcription factors (TFs), also known as trans-acting factors, are proteins with special structures that regulate plant growth and development. Transcription factors bind to specific DNA sequences (cis-acting elements) in the upstream promoter region of target genes through their DNA-binding domain (DBD), thereby regulating the specific expression of target genes in different cell types of plants or under different environmental conditions [1]. In plant morphogenesis, selective expression of genes leads to the differentiation of phenotypes, and transcription factors play an important regulatory role in these processes. TFs are divided into different gene families, such as the bHLH, TCP, MADS, bZIP, KNOX, WOX, AP2/ERF, NAC, GATA and ARF families, according to differences in DNA-binding domains and conserved motifs.

Shoot branching is a common phenomenon in plant growth and plays a very important role in plant morphogenesis. Branching also affects plant competitiveness against weeds or pests [2,3]. Therefore, research on branching mechanisms has become a popular topic worldwide. Studies have shown that axillary meristems initiate from cell groups detached from the primary SAM that retain their meristematic identity (Figure 1). Alternatively, axillary meristems may originate de novo later in development from partially or fully differentiated cells. Development of the lateral branch involves two important processes, axillary meristem formation and axillary bud growth [4,5].
Figure 1. Steps of plant shoot branching. (a) indicates the axillary meristem at the leaf primordium axis. (b) indicates the formation of axillary meristems (area shown in yellow box in (a)). (c) represents the development of plant axillary meristem into young branches.

Table 1. Transcription factors involved in regulating plant branching.

| Name                      | Homologs in Other Species | Family | Function                                                                 |
|---------------------------|----------------------------|--------|--------------------------------------------------------------------------|
| AtAGL6 (AGAMOUS-LIKE6)    |                             | MADS   | Facilitates the formation of axillary meristems                          |
|                           | OsMADS34                   |        | Coordinates with LAX1 to regulate the number of primary branches          |
|                           | OsMADS57                   |        | Is expressed predominantly in the SAM and axillary buds and is           |
|                           |                            |        | involved in SL signaling to enhance axillary bud growth and              |
|                           |                            |        | subsequent tillering                                                   |
| AtFUL (FRUITFULL)         |                            |        | Is involved in development of the axillary meristem, the expression of   |
|                           |                            |        | which is controlled by auxin                                            |
|                           |                            |        | Is negatively regulated by BRs and involved in AM initiation            |
|                            |                            |        | Is involved in initiation or                                           |
|                            |                            |        | maintenance of undifferentiated cell                                   |
| AtCUC1-3 (CUP SHAPED      |                            | NAC    | Facilitates the formation of axillary meristems                          |
| COYLEDON1-3)              |                            |        | Coordinates with LAX1 to regulate the number of primary branches          |
| AtSTM (SHOOT MERISTEMLESS)| OsOSH1 (O. sativa           | HB-KNOX | Is involved in lateral organ separation and axillary meristem            |
|                           | homeobox1)                 |        | formation                                                               |
| AtLOF1 (LATERAL ORGAN     |                            | MYB    | Inhibits branching and                                                  |
| FUSION1)                  |                            |        | downregulates STM when cells                                           |
| AtLOF2 (LATERAL ORGAN     |                            |        | start to differentiate                                                 |
| FUSION2)                  |                            |        |                                                                           |
| AtAS1 (ASYMMETRIC LEAVES1)|                            |        |                                                                           |
Table 1. Cont.

| Name | Homologs in Other Species | Family | Function |
|------|---------------------------|--------|----------|
| AtRAX1 (REGULATOR OF AXILLARY MERISTEMS 1) | Bl (Blind), S. lycopersicum | | Is involved in the early steps of AM initiation and development |
| AtRAX2-3 | | | Inhibits collateral growth |
| MsMYB112 | | | Inhibits branching and reduces cytokinin concentrations by inhibiting expression of IPTs in Arabidopsis |
| AtMYB2 | | | Promotes branching and is involved in maintenance of meristematic stem cell function and regulation of cell division |
| AtWUS (WUSCHEL) | OsTAB1 (TILLERS ABSENT1); OsMOC3 (MONOCULM 3) | WOX | Is involved in AM initiation |
| OsWOX4 | | | Regulates Arabidopsis secondary growth by SL signaling |
| AtWOX4 | | | Regulates branching by inhibiting the activity of MdTCP12 (BRC2 homolog) |
| MdWUS2 (WUSCHEL 2) | Ls, S. lycopersicum; ERA (ERAMOSA, A. majus); OsMOC1; HaLSL (LATERAL SUPPRESSOR LIKE) | GRAS | Is necessary for maintenance of the meristematic potential of the cells in the axils of leaf primordia |
| AtLAS (LATERAL SUPPRESSOR) | ZmBA1 (BARREN STALK1); OsLAX1 (Lax Panicle 1); AtROX (REGULATOR OF AXILLARY MERISTEM FORMATION) | bHLH | Is involved in development of the SAM and lateral young leaf primordia |
| HaROXL (REGULATOR OF AXILLARY MERISTEM FORMATION LIKE) | | | Is involved in development of the SAM and lateral young leaf primordia |
| OsLAX2 (LAX PANICLE2) | ZmBD1; COM2, H. vulgare | | |
| AtPIF4/5 (PHYTOCHROME INTERACTING FACTORS 4/5) | | | Inhibits the branching caused by phyB dysfunction and low R:FR |
| OsFZP (FRIZZLE PANICLE) | | | Represses axillary meristem formation |
| AtEBE (ERF BUD ENHANCER) | | AP2/ERF-ERF | Is involved in cell proliferation and axillary bud growth |
| AtDRN (DORNROSCHEN) | OsAPO2 (PANICLE ORGANIZATION 2) | | Regulates STM expression and AM initiation |
| AtDRNL (DORNROSCHEN-LIKE) | | | Is involved in cytokinin control of stem branching |
| AtERF053 | | | Promotes AM specificity through its action on LAX1 and CUC genes |
| OsRFL (RICE FLORICULA/LEAFY) | | | Promotes the formation of lateral meristems (e.g., branches) and axillary organs (e.g., leaf pillows) in wild-type maize |
| ZmBAD1 (BRANCH ANGLE DEFECTIVE1) | OsTB1 (TEOSINTE BRANCHED 1); OsFC1 (FINECULM1); VvBRC | TCP | Negatively regulates axillary bud growth |
| AtBRC1 (BRANCHED1) | MdTCP12 | | Has a redundant role with BRC1 in regulation of axillary bud growth |
| AtBRC2 (BRANCHED2) | | | Inhibits branching and downregulates STM when cells start to differentiate |
| AtAS2 (ASYMMETRIC LEAVES1) | | | |

*Note: All homologs are involved in meristematic cell proliferation and axillary bud growth.*
Table 1. Cont.

| Name | Homologs in Other Species | Family | Function |
|------|--------------------------|--------|----------|
| AtLOB1 (LATERAL ORGAN BOUNDARIES 1) | | | Is negatively regulated by BRs to reduce cell division and expansion in the border zone |
| AtWRKY71/EXB1 WRKY72 | | WRKY | Is expressed in tissues surrounding the AM start site |
| AtREV (REVOLUTA) | | HD-ZIP | Positively regulates bud branching |
| HB21 (Homeobox21) | | | Upregulates STM expression and promotes AM initiation |
| HB40 (Homeobox40) | | | |
| HB53 (Homeobox53) | | | |
| AtSPL13 (SQUAMOSA PROMOTER BINDING PROTEIN-LIKE 13) | | SBP | Inhibits branching, directly downstream of BRC1 |
| AtIPA1 (IDEAL PLANT ARCHITECTUREL1) | OsSPL14 | | Acts with D53 to mediate SL-regulated tiller development in rice |
| AtARR1 (ARABIDOPSIS RESPONSE REGULATOR 1) | | GARP-ARR-B | Downstream of cytokinins and promotes LAS expression by binding to their promoters |
| AtBES1 (BRI1-EMS-SUPPRESSOR1) | | BES1 | Inhibits branching and negatively regulates cambium activity in the SL signaling pathway in Arabidopsis |

Note: The transcription factor prefix indicates the species to which it belongs. At—Arabidopsis thaliana; Os—Oryza sativa; Ha—Helianthus annuus; Cr—Ceratopteris richardii; Zm—Zea mays; Sl—Solanum lycopersicum; Md—Malus pumila; Vv—Vitis vinifera.

In this review, we begin with the formation and growth of axillary meristems to elaborate on the research progress of transcription factors involved in regulating plant branching development to provide target genes for manipulating plant branching.

2. Axillary Meristem Formation

The first step of branching is the development of axillary meristems in leaves. In recent years, a series of transcription factors that regulate the initiation of leaf axil meristems have been found in Arabidopsis, rice, maize and tomato. The AM is formed in the center of the frontal boundary zone of the leaf base. This region is not only a boundary but also plays an important role in the maintenance of meristem and organ development [9].

The origin of AMs is a controversial topic. There is a major view that AMs originate from meristem cell groups that become detached from the shoot apical meristem (SAM) as leaves form and never lose their meristem identity [10]. Early AM development depends on the maintenance of the specificity and meristem ability of axillary cells. In Arabidopsis (Figure 2), WUSCHEL (WUS) is a homologous domain transcription factor that is expressed in the center of the SAM and specifies the fate of meristem cells in this region. The wus mutation leads to an inability to maintain stem cell division ability [11]. ARABIDOPSIS RESPONSE REGULATOR 1 (ARR1) is a transcription factor downstream of CK that promotes LAS expression by binding to its promoter, promoting AM initiation [12,13]. Cytokinins also activate WUS expression through ARR1, enabling stem cell differentiation and axillary bud formation [14].

MERISTEMLESS (STM) is another important factor for maintaining branch organization. STM, a KNOX gene, is expressed in the whole SAM but is excluded from the organ primordium that maintains the function of undifferentiated cells in the SAM [15]. The molecular markers of the AM include concentrated and strong expression of STM in the center of the boundary region [16]. Once cells begin to differentiate, STM is downregulated by the MYB family transcription factorASYMMETRIC LEAVES1 (AS1) and the LBD family
transcription factor AS2 [17]. This indicates that the cells in the border region maintain the ability to recover to the meristem stage within a limited period of time. During the developmental stage, AMs began to form [18].

Before axillary bud formation, REVOLUTA (REV) upregulates STM expression and promotes AM initiation. Subsequently, CK reactivates WUS expression to establish the AM [1]. Preliminary evidence shows that REV acts upstream of STM and WUS and that Ls/LAS acts upstream of STM to activate expression [19,20]. However, the upstream region of REV is regulated by LAS. As an HD-ZIP transcription factor, REV itself is necessary for all lateral meristem formation. In addition to RNA accumulation in other modes, REV is expressed in the near-axis position of the developmental leaf primordium in a region similar to RAX1, which can produce the position signal of RAX1 expression and control the radial mode [21,22]. The AP2 family transcription factor DORNROSCHEN (DRN) also plays a role in embryonic meristem and lateral organ development. Although AM initiation is affected in the drn-1 mutant, the drn-1 drnl-1 double mutant shows more serious defects in axillary bud formation than the single mutant, indicating that drn and drnl have important redundant functions in AM initiation [1]. Further studies have shown that DRN and DRNL preferentially affect the initiation pathway of the AM at the early nutritional stage rather than at late and reproductive stages. DRN, DRNL and REV can directly activate STM expression by binding to the same promoter region. In summary, DRN and DRNL redundantly promote AM initiation at the vegetative growth stage, and DRN/DRNL and REV synergistically upregulate STM transcription in mature leaf axils [23].

REGULATOR OF AXILLARY MERistem formation (ROX) encodes direct homologs of bHLH transcription factors, namely, LAX1 and BA1. In these mutants, axillary bud formation during vegetative bud development is damaged, and their combination with REGULATOR OF AXILLARY MERISTEMS1 (rax1) and las mutations enhance these branching defects [24], indicating that ROX regulates AM formation by cooperating with RAX1 and LAS [18]. In the nutritional and reproductive development process, orthologous bHLH transcription factors seem to be involved in the formation of boundary regions in eudicotyledons and Gramineae plants, as delayed growth is needed. In subsequent studies, ABA was found to significantly inhibit the expression of the RAX1 and LAS genes, thereby affecting the growth of axillary buds. RAX1 is a member of the largest MYB TF R2R3-MYB family in Arabidopsis. RAX2 and RAX3 genes function in the early stages of AM formation in rice, indicating that the BLIND/RAX pathway is unique to true dicotyledonous plants [31]. It should show that these genes are highly conserved [20,22,27]. Double mutants of las [21,22], which can produce the position signal of the same family, and ellipses represent genes other than transcription factors. The arrow and rough line represent positive and negative regulation, respectively.

**Figure 2.** The pattern of transcription factors involved in regulating axillary meristem formation in Arabidopsis thaliana. The rectangular box represents a transcription factor, the same color represents the same family, and ellipses represent genes other than transcription factors. The arrow and rough line represent positive and negative regulation, respectively.
initiation and development [22,24,25]. In addition, RAX1 promotes the early stage of AM formation; it also negatively regulates the gibberellin level in shoot tips to modulate AM formation and affect the timing of development phase transition [26]. Studies have shown that RAX1 is involved in the determination of axillary meristems by generating a tissue environment conducive to the establishment of meristems to control the spatial pattern of AM development [22]. In sunflower, the rax-like gene R2R3-MYB2 was also found to play a key role in AM formation to establish or maintain the leaf axillary stem cell niche [24]. The three genes are expressed at the regional boundary between the shoot apical meristem and leaf primordium prior to the establishment of axillary meristem [22]. Further evidence shows that LAS and RAX1 can replace ROX to some extent and regulate axillary meristem formation [27].

LATERAL ORGAN FUSION1 (LOF1) and LOF2 encode MYB transcription factors that play roles in lateral organ separation and axillary meristem formation, partly through interaction with CUC2, CUC3 and STM [16,28]. LOF1 is expressed at organ boundaries and acts upstream of RAX1, LAS and CUC [16,29,30]. The lof1 mutant exhibits defects in organ separation, which is the result of abnormal cell division and amplification during early boundary formation. In addition, low concentrations of BRs in the border area promote specific expression of the CUC gene and initiation of the AM [21].

The NAC domain proteins CUP SHAPED COTYLEDON1 (CUC1), CUC2 and CUC3 are involved in the initiation of the Arabidopsis SAM via STM expression [16,22,27,28]. The number of axillary buds in its mutants is significantly decreased [31]. Among the three CUC family members, CUC3 plays a major role in determining the formation and location of axillary meristems [30–32]. Further studies have shown that CUC1 and CUC2 control the development of the axillary meristem by regulating LAS and that CUC3 may play a role independent of LAS [30]. CUC2 is also regulated by RAX1 in early AM development to establish or maintain the stem cell niche formed by the AM [22,31]. In particular, transcription of CUC2 is continuously downregulated in the rax1 mutant, indicating that RAX1 affects AM initiation by regulating the expression of CUC2 [21]. Thus, RICE FLORICULA/LEAFY (RFL) promote AM specificity through an effect on LAX1 and CUC [33]. RFL is expressed in the vegetative axillary meristem and very young tillering buds, and its expression pattern is similar to that of STM, which may be related to the maintenance of the meristem cell zone [34].

Guo et al. [35] identified the EXCESSIVE BRANCHES1 (EXB1) gene, which encodes a WRKY transcription factor previously known as WRKY71 that is mainly expressed in tissues around the AM initiation site. The functional exb1-D mutant displays an obvious increase in branching, which is due to the combined effect of excessive AM priming and increased bud activity. Quantitative data show that EXB1 controls the initiation of the AM by positively regulating the transcription of RAX1, RAX2 and RAX3. Subsequent data indicate that EXB1 may be located upstream of the RAX gene and regulate AM formation [21,36]. EXB1 also regulates branching in Arabidopsis through negative regulation of auxin signaling [37]. Auxin is a well-known bud growth inhibitor, and AM initiation requires minimal auxin [28,38]. In the presence of apical buds exist, auxin is transported from top to bottom in the axilla and inhibits the growth of axillary buds. This phenomenon is called apical dominance [39]. WRKY proteins in the EXB1 clade regulate auxin pathways. Similarly, overexpression of rice WRKY72 in Arabidopsis also increases bud branching, suggesting that the role of EXB1 in bud branching may be evolutionarily conserved between monocots and dicots [40]. Furthermore, a key factor in the establishment of the AM boundary region in Arabidopsis is the transcription factor LATERAL ORGAN BOUNDARYES1 (LOB1), which induces PHYB ACTIVATION TAGGED SUPPRESSOR1 (BAS1) expression and encodes a protein that brassinosteroid-inactivation capacity. In leaf axils, BR accumulation is negatively regulated by LOB1, an important boundary-specific transcription factor [18]. LOB1 directly upregulates BAS1 to produce low BR concentrations to reduce cell division and expansion in border areas [21]. Unlike all other known regulators, AGAMOUS-LIKE 6 (AGL6) specifically promotes stem branching only at the leaf axils of stem leaves in Arabidopsis [41].
Similarly, in rice, TILLERS ABSENT1 (TAB1) and WUSCHEL-RELATED HOMEOBOX4 (WOX4) are two WUS genes that are necessary for AM initiation [31]. TAB1 is normally expressed only in the anterior portion of the meristem and is not usually expressed in the SAM or mature AM [42]. Interestingly, wus mutation does not affect axillary meristem development in Arabidopsis, but rice TAB1 seems to control AM formation through mechanisms different from those of WUS in Arabidopsis [43]. The other WUS family transcription factor, WOX4 (the close paralogous homolog of TAB1), plays a role in the development of the AM by alternating with TAB1 [44]. However, unlike TAB1, WOX4 is not expressed in the premeristem but contributes to the maintenance of the AM after almost complete AM establishment. TAB1 forms an AM by enhancing the expression of O. sativa homeobox 1 (OSH1) and WOX4 [31]. During rice AM formation, OSH1 is preferentially expressed in the AM, and a significant decrease in its expression and a decrease in tillering in its mutant indicate that the gene is necessary for the initiation or maintenance of the fate of undifferentiated cells at the very early stages of AM formation [45]. MONOCULM 3 (MOC3) is a direct homolog of WUS in rice and is necessary for the formation of tillering buds and interacts with key components of the CK pathway controlling rice tillering [46]. Cks antagonize auxin at the top. Even in the presence of auxin provided by the growing stem apex or the apex, CK applied to buds is sufficient to initiate growth [47].

LAX PANICLE1 (LAX1) and MONOCULM1 (MOC1) encode bHLH family and GRAS family transcription regulators, respectively, which are necessary for the initiation and maintenance of the AM in rice panicles [24,48]. LAX is expressed on the boundaries of apical meristem- and neomeristem-forming regions, specifically controlling the initiation or maintenance of new meristems [49]. Studies have shown a significant reduction in the number of spikelets in the lax1 mutant, and AMs cannot be formed during vegetative development. Similarly, the maize barren stalk1 (ba1) mutant cannot initiate AMs at any stage of the life cycle [24,50]. These two genes accumulate at the proximal axis boundary of the axillary meristems formed during nutrition and reproductive development [27]. MAD534 in rice encodes a MADS-box transcription factor that coregulates the number of primary and secondary branches with LAX1 [51]. MOC1 (a direct homolog of LATERAL SUPPRESSOR, LS in tomato and LATERAL SUPPRESSOR, LAS in Arabidopsis) was the first key transcription factor identified [52,53] controlling rice tillering; it is mainly expressed in leaf axils and axillary buds during AM development, positively regulating rice tillering [43,54]. As expression of MOC1 and LAX1 is not altered in the tab 1 mutant, TAB1 plays a role in an independent pathway or downstream of MOC1 and LAX1. In addition, LAX2, together with LAX1 and MOC1, plays a role in different AM maintenance pathways to control branching at vegetative and reproductive stages [45]. Similarly, disruption of LAS in Arabidopsis leads to AM loss during vegetative development, causing loss of branching or tillering and indicating that these genes are highly conserved [5]. In conclusion, both LAS and MOC1 are specifically expressed in the initiation region of the AM [21]. However, in the moc1 mutant, which lacks axillary buds and tillers, OSH1 expression completely disappears in leaf axils but is not affected in the SAM. Moreover, MOC1 is expressed earlier than LAX1, LAX2 and TAB1 during AM formation, indicating that the sequence or independent role of these genes is the cause of axillary bud formation and that multiple pathways contribute to the development of the AM [31].

Similarly, REGULATOR OF AXILLARY MERISTEM FORMATION LIKE (ROXL) isolated from sunflower is a homologous gene of ROX/LAX1. In situ results of a cross-section show accumulation of ROXL transcripts at specific points in the boundary region between the apical meristem and the lateral leaf primordium, displaying a similar pattern in Arabidopsis [27]. Based on in situ hybridization, Ha-ROXL exhibits clear-boundary transcription in vegetative branches, though the expression pattern of LATERAL SUPPRESSOR LIKE (LSL) is confined to the boundary region because signals can also be detected in other cellular domains of vegetative and reproductive branches. Transcription of LSL is also expanded at the early stage of lateral primordium development, indicating that this gene is
involved in the early development of the lateral primordium and in the initiation of the AM [24,55].

**BLIND (Bl)** is the homologous gene of the **RAX1** gene in tomato and **Arabidopsis** [21,25]. It encodes an R2R3 Myb transcription factor and regulates the early steps of AM initiation. There are fewer axillary buds due to defects in AM initiation caused by the **bl** mutant [31]. Double-mutation analysis has shown that different members of the Bl-related subgroup of the R2R3 Myb gene regulate axillary meristem formation in a partially redundant manner [22]. Double mutants of **ls** and **bl** in tomato display an additive phenotype, suggesting that at least two pathways are involved in AM initiation [20,22,27]. It is noteworthy that these genes are expressed in leaf axils during AM development. The homologous compounds of BLIND and RAX do not play a role in AM formation in rice, indicating that the BLIND/RAX pathway is unique to true dicotyledonous plants [31]. It should also be noted that in rice, axillary meristems usually develop into tillers from the basal nodes of plants, forming a typical cluster plant structure [34]. **FRIZZLE P ANICLE (FZP)** is a very important gene in rice tillering development. Its overexpression inhibits **RFL/PANICLE ORGANIZATION 2 (APO2)**, which suppresses the formation of axillary meristems at the vegetative stage and leads to a significant decrease in tiller number [48]. In maize, **BAD1** transcripts are detected mainly in the AM boundary region and between lateral branches, and its functional deficiency results in organ fusion via a reduction in the number and angle of branches [56]. Nevertheless, homologs of this gene, **COMPOSITUM 1 (COM1)** and **RETARDED P ALEA1 (REP1)**, in barley and rice have no similar functions. In addition, **BELL1-like homeobox 12 (BLH12)** and **BLH14** play an important role in maintaining axillary meristems and possess the redundant functions necessary for axillary bud development throughout nutritional and reproductive development [19].

In addition to common plants such as **Arabidopsis**, rice and maize, other species are predicted to have transcription factors involved in branching or tillering. For example, it was found that the formation of the AM in **Antirrhinum majus** requires **ERAMOSA (ERA)**, a gene encoding a GRAS transcription factor (orthologous to **LAS** in **Arabidopsis**). The basic role of **ERA** in AM formation is consistent with that of **LAS/MOC1/ERA** in preventing cell differentiation in the boundary area and in stimulating AM formation [57].

### 3. Axillary Meristem Outgrowth

The structure of mature plants is determined by the occurrence of axillary meristems, control of bud growth and subsequent dynamics of branching growth. Changes in these parameters result in the high morphological diversity observed in different plant species and even among individuals of a particular species [18]. After the formation of the AM, its growth as a branch repeats the development pattern of primary branches and endows plants with a branching structure [33]. Although a series of genetic studies have revealed the molecular mechanism and genes involved in SAM formation and maintenance, little is known about the generation and growth control of axillary buds [20].

The transcription factor **BRANCHRED1 (BRC1)** in **Arabidopsis** is homologous to **TEOSINTE BRANCHED 1 (TB1)** in maize and plays a core inhibitory role in regulating axillary bud growth (Figure 3). **BRC2** is a paralog of **BRC1**, which is also expressed in axillary buds and plays a redundant role in the regulation of axillary bud growth [43]. Similarly, **VvBRC** plays a key and negative role in branching in grape [58]. **LAS** and **REV** act upstream of **BRC1**. As expression of **BRC1** is significantly downregulated in the **max2** mutant, the **MAX**-mediated pathway seems to control the activity of **BRC1** [59]. **Homeobox 21 (HB21)**, **HB40** and **HB53** act directly downstream of **BRC1** to regulate branching [60]. Moreover, **BRC1** was identified as an inhibitor of downstream branches of SL signal transduction [61,62]. **SL**, a plant hormone synthesized by carotenoid catabolism, moves from root to stem, inhibiting stem branching by preventing the growth of axillary buds [63]. In **Arabidopsis**, another transcription factor involved in the SL pathway, namely, **BRI1-EMS-SUPPRESSOR1 (BES1)**, negatively regulates cambium activity in the SL signaling pathway. Further studies have shown that SL signaling regulates the expression level of **WOX4** through **BES1**, controlling secondary
growth [64]. CK is another class of hormones that has an important role in regulating apical dominance and axillary bud outgrowth. At the later stage of development, MYB2 reduces the concentration of CK by inhibiting the expression of IPTs, suppressing the growth of axillary buds [47]. In functional exploration of the MADS domain factor FRUITFULL (FUL) in Arabidopsis thaliana, it was found that the combination of auxin and BR strongly induced the growth regulator SMALL AUXIN UPREGULATED RNA 10 (SAUR10) to be directly modulated by FUL, thus participating in branching angle regulation [65]. It should be noted that FUL also responds to a decrease in R:FR light by regulating the SAUR10 pathway and affecting Arabidopsis branching [65]. The auxin-regulated branching pathway in Arabidopsis involves a class of photochrome-targeted transcription factors, PHYTOCHROME INTERACTING FACTOR 4 (PIF4)/PIF5 [66]. When these transcription factors participate in photoreactions, they inhibit the branching caused by phyB dysfunction and low R:FR. Hence, R:FR plays an important role in branching.

Figure 3. Patterns of transcription factors involved in regulating axillary meristem growth in Arabidopsis thaliana. The rectangular box represents transcription factors, the same color represents the same family, and ellipses represent genes other than transcription factors. The arrow and rough line represent positive and negative regulation, respectively.

Overall, the interaction between ABA and auxin may mediate the effect of PIF4/PIF5 on branching [67]. Mohammad et al. [68] reported another transcription factor, ERF BUD ENHANCER (EBE), that affects cell proliferation, axillary bud growth and branching in Arabidopsis. The gene encodes the AP2/ERF transcription factor and is strongly expressed in proliferating cells. Moreover, overexpression of EBE promotes cell proliferation, shortens the cell cycle in growing calli and stimulates the formation and growth of axillary buds [68].

TB1, also known as FINECULM1 (FC1), is a TCP family transcription factor that negatively regulates rice tillering and inhibits the subsequent growth of axillary buds [69]. This gene encodes a TCP TF that is expressed at the base of these buds and SAMs. Its overexpression leads to a significant reduction in tiller number, whereas the tb1 mutant exhibits an increase in tiller number [31]. In addition, TB1 may be a common target for the CK and SL pathways and act downstream of SL [70,71]. MADS57 is a transcription factor of the MADS domain family that participates in the regulation of axillary bud growth in rice. RNA in situ hybridization analysis has shown that MADS57 is mainly expressed in meristems and axillary buds. Additionally, its expression is higher in the tillering and stem elongation stages than in other stages of rice growth [70]. Interaction of TB1 with MADS57 reduces the negative regulatory activity of MADS57 on D14 expression, allowing MADS57 to affect tillering [71].
In a study of branching-related genes in chrysanthemum, *CmERF053* was found to be rapidly upregulated in axillary buds when apical dominance was relieved, which may be related to the growth of lateral branches. The gene belongs to the AP2/ERF family and is mainly expressed in stem and root organs. Further transcriptome analysis showed that CK-mediated control of stem branching may be related to the transcription level of *CmERF053* [26]. *IDEAL PLANT ARCHITECTURE1* (IP A1), also known as *SQUAMOSA PROMOTER BINDING PROTEIN-LIKE 14* (SPL14), is another key regulator that determines plant structure but not meristem activity, and upregulation of *IPA1* expression leads to fewer tillers in rice [72]. Furthermore, *IPA1* overexpression lines display a reduced tillering phenotype, whereas tillering in the *ipa1* mutant increases [73]. This gene acts as a direct downstream component of *D53* in regulating tiller number and SL-induced gene expression. In fact, *D53* is one of the only known transcription targets of SL, and *D53* inhibits *IPA1* upregulation [74]. *IPA1* directly binds to the *D53* promoter and plays a key role in the feedback regulation of SL-induced *D53* expression. In summary, *IPA1* may constitute a long-term transcription factor that acts with *D53* to mediate SL-regulated rice tillering development [75]. In later vegetative axillary bud growth, *OsMADS57* enhances axillary bud growth and subsequent tillering through SL signal transduction via direct inhibition of expression. *OsMADS57* directly inhibits *D14* transcription to regulate tillering during organogenesis [70].

The *SQUAMOSA PROMOTER BINDING PROTEIN-LIKE 13* (SPL13) gene encodes an SBP transcription factor that is mainly expressed in meristems and is essential for regulating branching and vegetative growth in *Medicago* [63]. Overexpression of *SPL13* inhibits axillary bud growth, thereby reducing lateral branches. In this process, *MYB112* is targeted and downregulated by *SPL13*. Compared with WT, *MsMYB112* RNAi plants show more branches, which confirms that *MYB112* itself also inhibits the lateral branch growth of alfalfa [63,76]. Furthermore, *MdWUS2* in apple can regulate branches by inhibiting the expression of *MdTCP12* [77].

*Related to ABI3 and Viviparous 1* (RAV1) is a circadian rhythm gene in *Castanea mollissima* that is homologous to the *TEM* gene in *Arabidopsis*. It reaches its peak expression at noon under vegetative growth conditions and is highly expressed during winter dormancy and in response to low temperature [78]. When the CsRAV1 protein was overexpressed in hybrid poplar, high sylleptic branching was induced during the same growing season as lateral bud formation.

### 4. Application of Branching-Regulating TFs

Genetic control of branches is the main determinant of yield, seed number regulation and harvestability. For example, interference mutations in *FZP* and *IPA1* in rice, *TB1* in maize, and *BRC* in grape lead to increased branching and increasing yield [20,48,75,79]. Overexpression of *Bl* in tomato increases the number of branches, also increasing yield. At the same time, the change in plant type caused by branching provides an opportunity to explore the ornamental value of plants. For example, overexpression of *CmERF053* significantly increases the number of branches in chrysanthemum. In summary, regulation of these key transcription factors can significantly increase the number of branches, thereby increasing crop yield or quality.

In addition, fine regulation of branching has become an important strategy for plants to morphologically adapt to various environments. Chestnut CsRAV1, a circadian rhythm response factor, participates in the winter dormancy and low-temperature response of poplar and increases branching. Thus, manipulating this gene may lead to the possibility of producing trees with greater biomass. In actual cultivation, plants usually inhibit axillary bud growth in response to reductions in the ratio of red light to far-red light (R:FR) caused by the presence of competitive neighbors. Overexpression of *PIF4* and *PIF5* significantly inhibit the branching caused by this shade-avoidance syndrome, providing opportunities for practical cultivation.
5. Environmental Pathways Involved in the Control of Shoot Branching

It is well known that plant types have remarkable plasticity. Branch development is affected by many external factors, such as light, temperature and soil nutrients. Light is a powerful environmental factor that affects the branching of plants [80]. For example, low-intensity light reduces tillering in *Triticum aestivum* [81], whereas high-intensity light increases branching in hybrid roses [82]. Low R:FR and a decrease in blue light intensity trigger SAS, which leads to a decrease in axillary bud growth ability, such as in *Rhododendron* and *Hordeum vulgare* [83]. However, in *Lilium*, FR light strongly inhibits bud outgrowth [84], and blue light can increase or decrease the length of branches and internodes [85]. In general, UV radiation exposure reduces the length of branches [86], and studies have shown that photoperiod is one of the environmental factors involved in regulating branching, altering the branching pattern [87]. In summary, light is of great significance for the regulation of branching. In addition to light, temperature, moisture, carbon dioxide and other environmental factors affect the branching of plants. High temperature can inhibit branching, and CO$_2$ reduces the negative impact of high temperature on branch growth [88].

Of course, water and nutrients (such as nitrogen and phosphorus) are decisive factors in regulating plant shoot branching [89]. Many TFs responding to plant stress responses have been reported. However, research on TFs involved in branch response stress is scarce. Therefore, further exploration of TFs involved in branching response stress is worthy of attention.

6. Perspectives

Branching determines plant architecture and crop yield and plays an important role in plant morphogenesis. Therefore, research on branching regulation mechanisms is a popular topic worldwide. The regulation of plant branching by different transcription factors through mutual connections is one of the main directions of the current study of branching development patterns. Previous research and discussion on a single transcription factor have been the premise and foundation for studying the transcription regulatory network.

Notably, the functions of some transcription factors are not conserved. For example, *RAV1* in chestnut is a circadian rhythm gene that is homologous to the *TEM* gene in *Arabidopsis*. However, the two genes may lead to different phenotypes in woody and herbaceous plants. In view of the transcription factors related to branching discovered to date, we found exploration of the new functions of known transcription factors to be innovative, even though conserved transcription factors appear to provide key targets for the branching regulation mechanism.

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