"Crop reproductive meristems in the genomic era, a brief overview"

Francesca Caselli[1], Fabio Zanarello[1], Martin M. Kater[1], Raffaella Battaglia[2], Veronica Gregis[1*]

[1] Department of Biosciences, University of Milan, Via Celoria 26, 20133 Milan, Italy
[2] CREA Research Centre for Genomics and Bioinformatics, 29017, Fiorenzuola d'Arda (PC), Italy

Contact information: *Email of corresponding author Veronica Gregis: veronica.gregis@unimi.it

ABSTRACT

Modulation of traits beneficial for cultivation and yield is one of the main goals of crop improvement. One of the targets for enhancing productivity is changing the architecture of inflorescences since in many species it determines fruit and seed yield. Inflorescence shape and organization is genetically established during the early stages of reproductive development and depends on the number, arrangement, activities, and duration of meristems during the reproductive phase of the plant life cycle. Despite the variety of inflorescence architectures observable in nature, many key aspects of inflorescence development are conserved among different species. For instance, the genetic network in charge of specifying the identity of the different reproductive meristems, which can be indeterminate or determinate, seems to be similar among distantly related species. The availability of a large number of published transcriptomic datasets for plants with different inflorescence architectures, allowed us to identify transcription factor gene families that are differentially expressed in determinate and indeterminate reproductive meristems. The data that we review here for Arabidopsis, rice, barley, wheat, and maize, particularly deepens our knowledge of their involvement in meristem identity specification.

INTRODUCTION

Crops are characterized by a striking variety of inflorescence types, determined by the coordinated activity of niches of undifferentiated stem cells, called meristems (Fig.1).
A mathematical "transient model" predicts that the final architecture of the inflorescence is determined by the fine-tuning of the proliferative activity of the indeterminate meristems (IMe), and their ability to differentiate into a determinate meristem (DMe) (1).
Stem cells homeostasis within the reproductive meristems is crucial to tailor inflorescence architecture and ultimately depends on the balance between meristematic cell population versus daughter cell differentiation. A feedback signaling loop is responsible for this equilibrium, and despite being mainly studied in Arabidopsis, this pathway seems to be broadly conserved across species such as maize, rice, and tomato (reviewed in (2)). Master players are WUSCHEL (WUS) and WUSCHEL-RELATED HOMEOBOX (WOX) and KNOTTED-LIKE HOMEOBOX (KNOX) transcription factors and CLAVATA leucine-rich repeat receptor-like kinases and their ligands. These factors modulate the transcription of target genes which include many genes involved in biosynthesis or signaling of phytohormones (3).

The dicot model species *Arabidopsis thaliana* has a raceme inflorescence, in which the indeterminate inflorescence meristem (IM) grows indeterminately producing on its flanks several determinate flower meristems (FMs), whose destiny unequivocally leads to flower formation and the depletion of meristematic cells (Fig. 1A). Cymose inflorescences, such as those of Solanaceae, are characterized by IM that ends with a

flower meristem and eventually produces a new IM on the side which reiterates the same developmental pattern. In grasses, the IM produces different meristem types which ultimately differentiate into a spikelet meristem (SM), producing florets that can be directly attached to the main inflorescence axis, as in spikes, or developing on flower-bearing branch meristems (BMs), as in panicles (4). Figure 1 describes the development and the architectures of reproductive meristems in Arabidopsis, rice, wheat, maize, and barley.
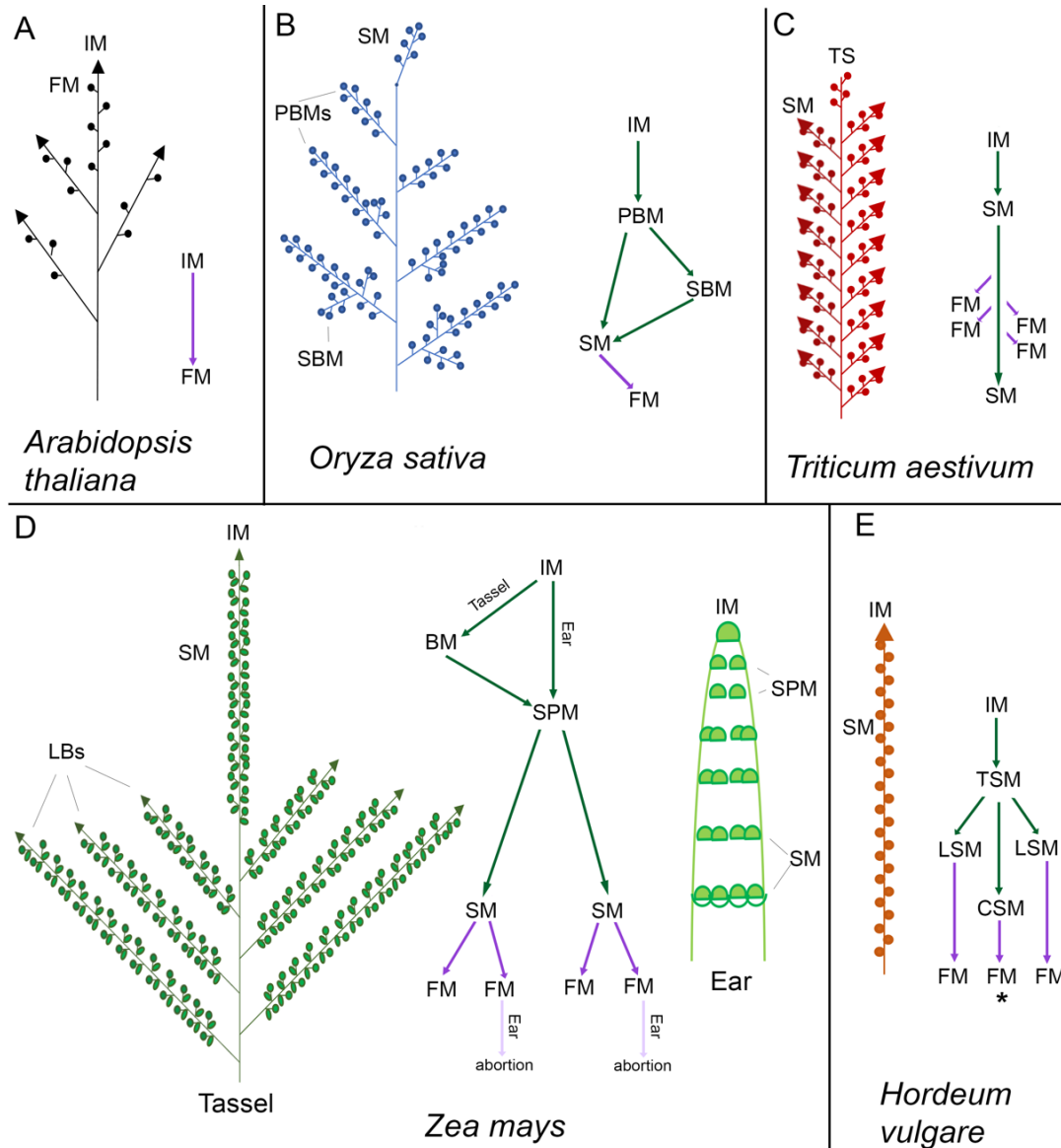

Figure 1. Scheme of inflorescence architecture and meristem identity transition with a graphical configuration of reproductive meristems development in (A) Arabidopsis, (B) rice, (C) wheat, (D) maize, and (E) barley. Circles: Determinate Meristem (DMe), arrows: Indeterminate Meristems (IMe).

(A) In Arabidopsis thaliana, the IMe lasts for the entire life of the plant and produces DMe which differentiates completely in FM.

(B) In the branched panicle of Oryza sativa, the IMe is called rachis meristem (RM). During inflorescence development, some cells of the IMe differentiate into the Primary Branch Meristems (PBMs) and Secondary BMs (SBMs) which produce and differentiate determinate SMs. IM elongates after the branches differentiation and aborts after producing a variable number of PBMs.

(C) In Triticum aestivum, the inflorescence is a determinate spike where the IMe differentiates into SMs which produce a variable number of FMs.

(D) In Zea mays two distinct inflorescences are produced, tassel and ear, which differentiate into male and female flowers, respectively. Both structures share a similar architecture in which an apical IMe develops a series of lateral meristems (LBs). The spikelet-pair meristem (SPM) initiates two spikelet meristems (SM), each of which develops two floral meristems (FMs); in ears, one FM undergoes a selective abortion. Contrary to the ear, the tassel is a branched inflorescence, in which the IM can differentiate both SPM and Branch Meristems (BM).
(E) In Hordeum vulgare, the Ie produces triple spikelet meristem (TSM) which differentiates in lateral spikelet meristems (LSM) and a central spikelet meristem (CSM). In two-rowed spikes, only the CSM produces a fertile flower (*) in six-rowed spikes LSMs, and CSM all differentiate fertile flowers.
Green arrow: IMe (Indeterminate Meristem) formation, purple arrow: DMe (Determinate Meristem) formation), pink arrow: abortion of floral meristems. Abbreviations: LB: lateral branch meristem; FM: floral meristem; IM: inflorescence meristem; LSM: lateral spikelet meristem; PBM: primary branch meristem; SBM: secondary branch meristem; SM: spikelet meristem: SPM: spikelet pair meristem; TSM: triple spikelet meristem; * FM which develops in two-rowed spikes.

The determination of meristem identity and the transition from indeterminate to determinate meristem activity are governed by a complex gene network of which some master regulators have been well characterized, but many others remain still unknown. Identifying new players in this complex process will provide a better understanding of the mechanisms through which the architecture of the inflorescence is determined and will facilitate crop improvement for traits like grain yield per hectare, which is closely linked to finding solutions to feed a fast-growing world population. Therefore, there is an increasing interest in understanding the regulatory networks underlying inflorescence development. The growing number of plant genomes that have been sequenced and annotated together with the huge number of transcriptome datasets, including meristem-specific ones, facilitate comparative analysis of meristem related datasets (5–13). Furthermore, inter-species comparative transcriptomic is rapidly gaining popularity, as it has been proven to be a useful tool both to discover common meristem regulators and to identify factors behind the divergences observed among different inflorescence architectures (9,11,12).

In this review, we summarize some of the knowledge acquired in the recent years on the master regulators of meristem determinacy and identity in some of the staple cereals species, focusing in particular on families of transcription factors, which are considered to be the major players in the evolution and domestication of crops. Because of their role in regulating gene expression, transcription factors are generally considered important targets of crop improvement, especially when dealing with multigenic traits (14,15).

To identify those families whose activity controls the specification of the different meristem types, we compared the transcriptomes generated from reproductive meristems of *Arabidopsis thaliana* (5), rice (multiple accessions) (9), maize (*Zea mays,* cv B73) (7), barley (*Hordeum vulgare,* cv Morex) (13) and bread wheat (*Triticum aestivum*, cv Chinese Spring) (8). In particular, since we wanted to specifically review the genetic pathway controlling the transition from indeterminate to determinate fate, we decided to prioritize the comparison between indeterminate meristem (IMe) and determinate meristem (DMe) transcriptomes (Fig. 2). We, therefore, selected datasets of Differentially Expressed Genes (DEGs), that were generated with a similar methodology: hand-dissection meristems with a morphological control to assess their developmental stage (Table 1). Because of the extensive knowledge available for *Arabidopsis thaliana*, the transcriptome generated from laser-dissected inflorescence meristems of this specie was also included in the analysis (5). We exploited the PLAZA database (16) to assign each DEG to a specific gene family and families coding for transcription factors (TF) were selected and grouped according to their functional domains. This strategy allowed us to extrapolate which TF families are differentially expressed during the transition from IMe to DMe.

The sets of families from the different species were then intersected, to extrapolate the number of families in common in all the possible comparisons between the selected species (Fig. 3). We were then able to visualize

common and species-specific gene families that might control meristem identity and determination during inflorescence differentiation.
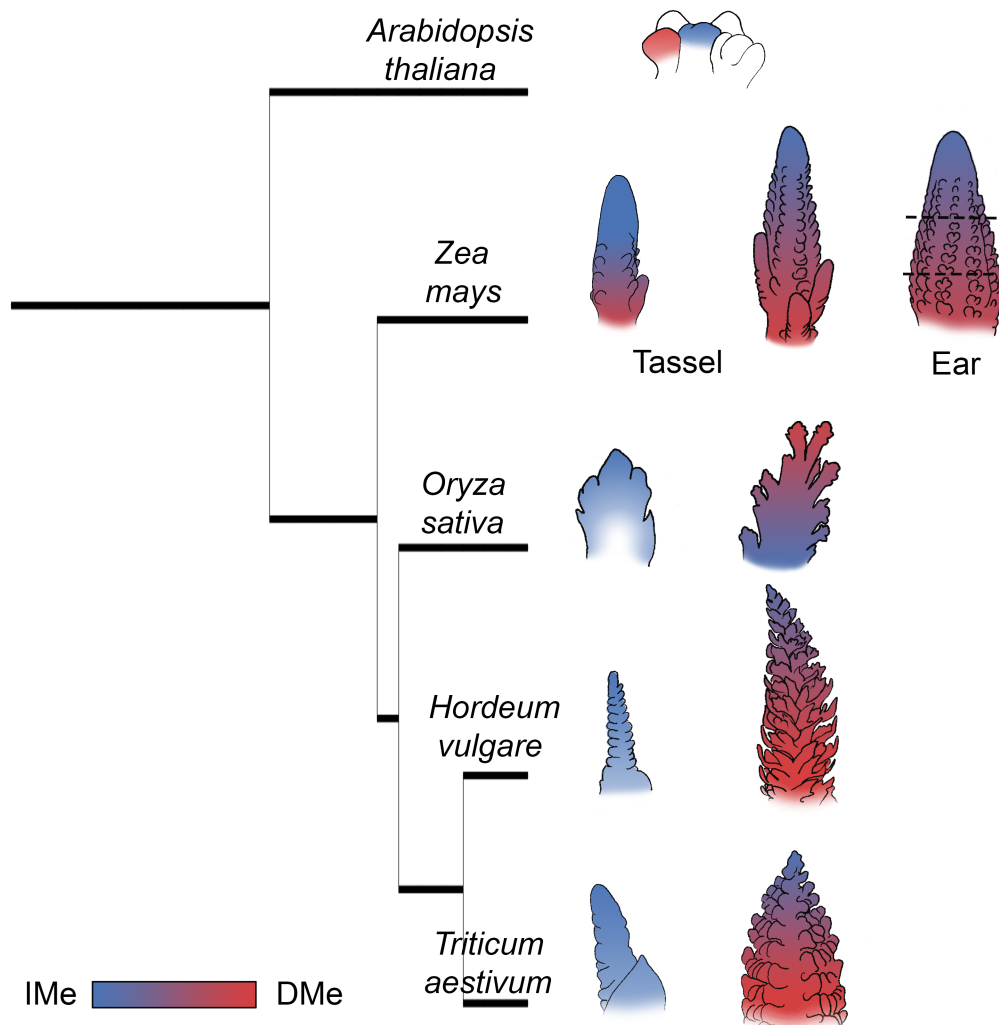

Arabidopsis thaliana

Zea mays

Tassel   Ear

Oryza sativa

Hordeum vulgare

IMe ▬▬▬ DMe

Triticum aestivum

Figure 2. *Schematic representation of the Indeterminate Meristems (IMe) and Determinate Meristems (DMe) sampled in Arabidopsis, rice, wheat, maize, and barley.*
The qualitative phylogenetic tree was produced and adapted from PhyloT (https://phylot.biobyte.de/) based on the NCBI taxonomy of the four species.
The draws represent the IMe-enriched samples (Blue) and DMe-enriched samples (Red) collected in the different experiments of RNAseq transcriptome analysis considered in this review.
In Arabidopsis, the IM (IMe) and FM (DMe) were sampled through laser-dissection, as indicated in the drawing. Zea mays tassels were hand dissected and separated, according to their dimensions, in IM/SPM (IMe enriched tissue) and SM (DMe enriched tissue). Ears were sectioned into different segments, as indicated by the dotted lines, into IM/SPM (IMe enriched tissue) and SM (DMe enriched tissue). Drawings were adapted from (6).
Oryza sativa meristems were hand dissected and classified according to their morphology, into indeterminate meristems (PBM and SBM) and determinate meristems (SM). Oryza sativa reproductive meristems were adapted from (9).
In Hordeum vulgare inflorescence meristems at double-ridge (DR) corresponding to the Waddington stage W2.0 (IMe) and awn primordium (AP), corresponding to W3.5(DMe), stages were collected. Drawings were adapted from (12).
Triticum aestivum meristems at Double Ridge (IMe) and FM (DMe) stages were collected. Drawings were modified from (7).
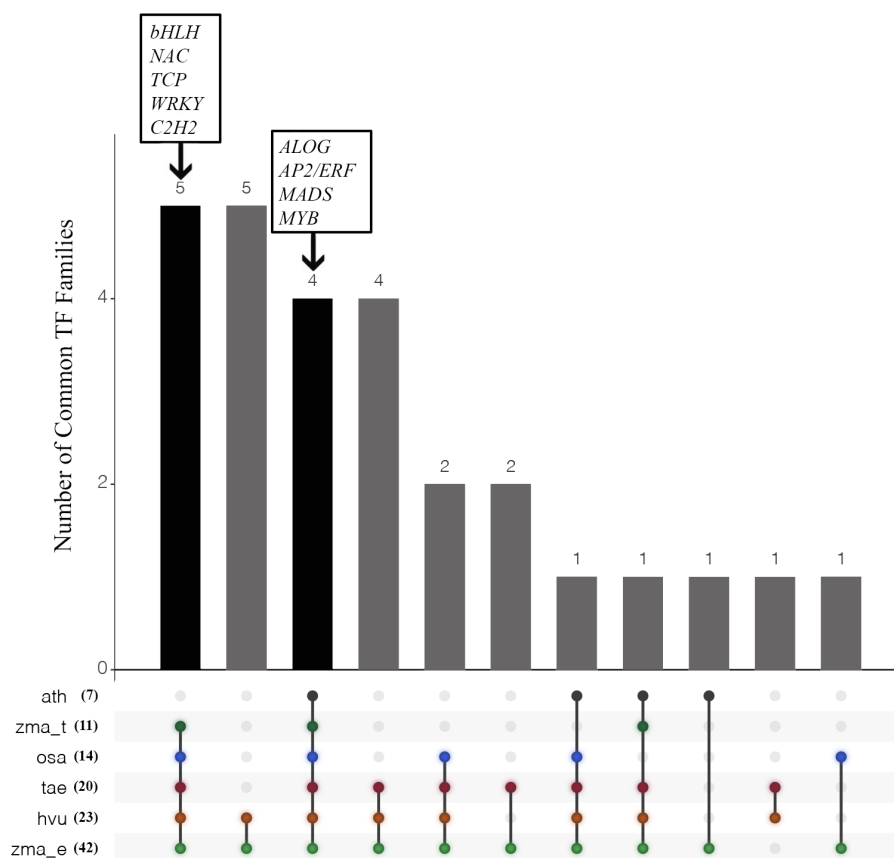
Intersecting Sets of Transcription Factor Families

Figure 3. *Intersecting sets of TF families of Arabidopsis, rice, wheat, barley, and maize (tassel and ear). All the different comparisons are shown with dots on the x-axis, the number in brackets indicates the number of TF families differentially expressed in each species. The histogram shows the number of detected TF families in common between the different transcriptomic sets considered in this review, the number of families for each comparison is indicated on top of each bar. The two black bars represent the intersections between rice, maize, barley, and wheat (the crop-specific regulators: NAC, TCP, WRKY, C2H2, and bHLH) and between all the species considered (common regulators: MADS; ALOG, AP2/ERF, and MYB).*
ath: Arabidopsis thaliana; osa: Oryza sativa; zma_t: Zea mays_tassel; tae: Triticum aestivum; hvu: Hordeum vulgare; zma_e: Zeam mays_ear. The plot was designed with the UpSetR package.

The GO enrichment analysis revealed that all the DEG lists are significantly enriched of terms as TF, expression regulation, DNA binding, RNA biosynthesis, and flower development. The list of DEG TF genes allowed us to identify four TF families, ALOG, AP2/ERF, MADS, and MYB, in the Arabidopsis, rice, wheat, barley, and maize transcriptomes (Fig 4A). The meristem transition from indeterminate to determinate is a crucial step in the life cycle of plants, as it strongly influences the final plant architecture. Despite the variety of inflorescence morphologies that characterize different species, this process is likely orchestrated by a conserved set of master regulators, which includes the TF families mentioned above.

From the analysis, we further defined a group of five cereal-specific TF families: *bHLH, NAC, TCP, WRKY*, and *C2H2* (Fig. 4B); we foresee that these factors could be putative targets for crop improvement.

Here, we reviewed the current knowledge on these two sets of conserved and cereal-specific TF families, deepening, in particular, their role in indeterminate vs determinate meristem development.

SPECIES (Ref)	IMe Indeterminate Meristem	DMe Determinate Meristem	Replicas	Sampling	SEQ technique	Cutoff (p value)	DEGs tot	% TF
Ath (5)	Inflorescence Meristem	Floral Meristem	3	laser dissection	Illumina 50-bp reads	0.05	46	26.09
Zma_t (7)	Inflorescence Meristem/ Spikelet Pair Meristem	Spikelet Meristem	2	hand dissection	Illumina 50-bp reads	0.05	144	13.89
Osa (9)	Primary Branch Meristem/ Axillary Meristem	Spikelet Meristem/ Floret Differentiation	3	hand dissection	Illumina 125-bp reads	0.05	130	27.69
Tae (8)	Double Ridge/ Spikelet Meristem	Floret Meristem	2	hand dissection	Illumina 50-bp reads	0.05	753	9.56
Hvu (13)	Double Ridge	Awn Primordium	3	hand dissection	Illumina 200-bp reads	0.05	702	16.38
Zma_e (7)	Inflorescence Meristem/ Spikelet Pair Meristem	Spikelet Meristem	2	hand dissection	Illumina 50-bp reads	0.05	8327	7.626

Table 1. *Sequencing information for the different datasets employed in this review.*
For each species, the tissues sampled in the Indeterminate Meristem (IMe) and Determinate Meristem (DMe) stages are briefly described. Sequencing information, DEGs number, and the percentage of TF in each DEG list are also indicated.

Conserved regulators among different species

A core of four transcription factor families, *MADS*, *ALOG*, *AP2/ERF*, and *MYB*, resulted differentially expressed in all the datasets that were reviewed in this work (Fig. 3 and Fig. 4A).

MADS-box transcription factors are implicated in several developmental processes in fungi, plants, and animals. The name of this family is an acronym of *MCM1* from *Saccharomyces cerevisiae*, *AG* from Arabidopsis, *DEFICIENS* from *Antirrhinum majus*, and *SRF* from *Homo sapiens,* the first MADS-box domain proteins to be discovered (17).
In the plant kingdom, these transcription factors are best known for their key role in the control of meristem identity specification and organ differentiation. Genome-wide analyses led to the characterization of this family in different plant model species, including crops (18–21). *MADS-box* genes are already well known as key regulators of inflorescence development and, for this reason, it was not surprising to find members of this family differentially expressed in all the meristems and species considered.
Since MADS-box gene functions and relevance in the context of inflorescence development and crop improvement have been recently reviewed (22–25), we will not further discuss this gene family.
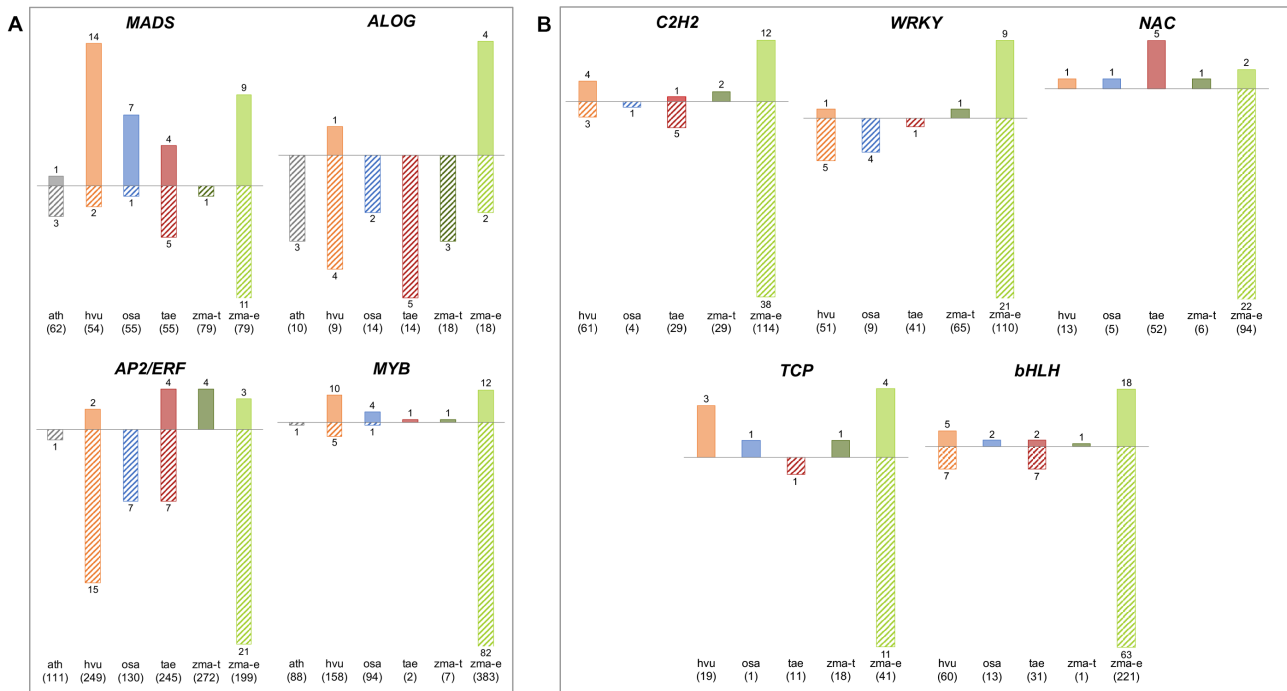
Figure 4. *Expression trend of the DEGs of the families described.*

The panels display the DEGs belonging to the different families here described, grouped in families with differentially expressed members in all the species considered (A) and only in monocots (B). The solid bars of each histogram shows the number of genes whose expression increases during the switch from indeterminate (IMe) to the determinate meristem (DMe), and the striped bars indicate the number of genes whose expression is higher in the indeterminate meristem (IMe). On the x-axis, the names of the species and the total number of genes belonging to the family are indicated. ath: Arabidopsis thaliana; osa: Oryza sativa; zma_t: Zea mays_tassel; tae: Triticum aestivum; hvu: Hordeum vulgare; zma_e: Zeam mays_ear

The *ALOG* genes encode plant-specific transcription factors named after the first two identified members of this family, *LHS1* in Arabidopsis and *G1* in rice. In Arabidopsis, *LSH1* was found to be involved in the light-dependent regulation of seedling growth (26). *LSH3* and *LSH4,* which are differentially expressed between the indeterminate and determinate meristems of Arabidopsis, are specifically expressed in the meristematic boundary cells. In these regions, they suppress organ differentiation and their expression is regulated by a boundary gene belonging to the *NAC* family, *CUC1* (*CUP-SHAPED COTYLEDON1*) (27,28).

Recently, in monocotyledons, genome-wide analyses led to the identification of several genes belonging to this family (29,30). Among these genes, the rice *TAWAWA1* (*TAW1*) is one of the few *ALOG* genes with a characterized role in inflorescence architecture determination. This transcription factor is expressed in the reproductive meristem and was proven to be necessary and sufficient to promote meristem indeterminacy, delaying its shift to SM. *TAW1* is a transcriptional activator, able to induce the expression of several *MADS-box* genes that are known to regulate BM maintenance. In the dominant *tawawa1-D* mutant, the BM can produce more branches before spikelet formation, leading to an increase in the total spikelet number and grain yield (31).

It is interesting to mention that, in the datasets considered for this review, the majority of the *ALOG* differentially expressed between IMe and DMe showed the same trend of expression, being downregulated as the meristem acquires a determinate identity (Fig. 4A). Although functional information is still missing for the maize, barley, and wheat *ALOG* gene family, it becomes tempting to speculate that these transcription factors share a similar role in the specification of the indeterminate reproductive meristems in distantly related species, thus being promising targets for crop improvement.

The APETALA2/Ethylene Response Factors belong to one of the largest superfamily of TFs in the plant kingdom. Based on the number of AP2/ERF domains and their sequence similarity, the members of this superfamily can be further divided into three groups: *AP2*, characterized by the presence of two AP2 domains, the *ERF*, with a single AP2 domain, and the *RAV*, which contains also a B3 DNA-binding domain. Members of this superfamily have been functionally studied in several species, including Arabidopsis, rice, and wheat (32–34).

In several plant species, a sub-group of AP2/ERF TFs has also been linked to the regulation of reproductive development (35). In Arabidopsis, for instance, *DORNRÖSCHEN, DORNRÖSCHEN-LIKE*, and *PUCHI* control floral meristem identity and organ number (36–38).

Recent transcriptomic data from wild and domesticated rice species revealed that the expression of several *AP2/ERF* genes strongly correlates with the domestication status and branching potential of the analyzed varieties, which indicates that the evolution of the ERF family was driven by artificial selection (9). Among the rice AP2/ERF transcription factors, the *PUCHI* homologous *FRIZZY PANICLE (FZP)/BRANCHED FLORETLESS1 (BFL1)* is considered one of the key regulators of SM determinacy (39–41). *FZP* expression is regulated by two AP2 genes, *SUPERNUMERARY BRACT* (*SNB*) and *OsINDETERMINATE SPIKELET1* (*OsIDS1*), which redundantly control the transition from SM to FM (42,43). Finally, *MULTI-FLORET SPIKELET1* (*MFS1*) was also found to be a regulator of spikelet meristem and flower development (44).

A similar role in the determinacy of SM branching and identity was also established for the maize AP2/ERF genes *BRANCHED SILKLESS1(BD1), INDETERMINATE SPIKELET1 (IDS1)* and *SISTER OF IDS1 (SID1)* (45,46). *IDS1* and *OsIDS1* activity is regulated with a similar mechanism, that involves the interaction with miR172 (47,48). Interestingly, an important role for AP2/miR172 in shaping the inflorescence structure has been described in different monocots and it is known that mutants in this pathway have been selected during crop domestication (49–52).

Even though the functional characterization of most of the AP2/ERF genes described suggests a role for these genes during later stages of spikelet meristem development, our comparative transcriptomic analysis highlighted the presence of a subset of AP2/ERF factors already active during the transition from indeterminate to determinate meristem. It would not be surprising to find that, overall, this gene family plays crucial roles throughout reproductive development, coordinating different steps that allow the progression of inflorescence differentiation.

The fourth family of common regulators is characterized by the presence of the MYB DNA-binding domain. MYB-containing proteins can be divided into four subfamilies, according to the type and number of repeats they contain. The R2R3-MYB subfamily is the most represented group in plants, with more than 100 identified in different species (53,54). This superfamily has been linked with the control of plant metabolism and to the response to biotic and abiotic stress in several species (55–59). A few members of this family were also found to be involved in the regulation of developmental processes such as flowering time (60,61), floral organ development (62) and shoot branching and axillary meristems formation (63).

Cereal-specific regulators

Interestingly, transcriptomic analysis of determinate and indeterminate meristems highlighted the presence of monocot-specific TF families differentially expressed between IMe and DMe. (Fig. 3 and 4B).-

Despite the knowledge that the activity of the maize RAMOSA genes is required to modulate branching (7,64), no C2H2 protein has yet been linked to this process in other species.

The C2H2 Zinc Finger proteins represent one of the largest family of transcriptional regulators in eukaryotic organisms and, in the plant kingdom, the majority of the characterized members of this family have been linked to abiotic stress response pathways (65–67).

An exception can be found in rice, where *STAMENLESS1 (SL1)* is known to be involved in flower development (68). Furthermore, two other members of this family, *EMBRYONIC FLOWER 2* (*OsEMF2)* and *ZINC FINGER PROTEIN 15* (*OsZFP15*) were shown to be specifically expressed during reproductive development, however, their function in these tissues is still unclear(69,70).

The observation that several members of this family are differentially expressed between indeterminate and determinate meristem in different cereal crops, in conjunction with the key role played by the RAMOSA3 factor in maize, suggests the possibility that a deeper analysis of the function of the C2H2 zinc finger transcription factors would uncover new mechanisms at the base of meristem identity determination and branching in these species.

From our transcriptome data analysis, a second family of zinc finger transcription factors, the *WRKY* family, was found to be differentially expressed in the comparison between indeterminate and determinate meristems in rice, maize, barley, and wheat even if the role of these genes in the regulation of plant reproductive development is still elusive.

The *WRKY* genes contain at least one repeat of the WRKY DNA-binding domain, which code for 60 highly conserved amino acidic residues, and a C2H2 or C2H2C zinc finger domain. Based on the number of WRKY domains and the structure of the zinc finger domain these proteins are divided into three different subgroups. WRKY transcription factors have been extensively studied in the model species Arabidopsis, as well as in several agronomic relevant crops, since they are considered to be key regulators of plant immunity and biotic and abiotic stress responses, but also in developmental processes such as seed development and senescence (71–77). Until now, a restricted number of *WRKY* genes have been linked to the control of agronomical relevant traits, like yield, in rice and maize (78–81).

The *NAC* genes have been extensively analyzed in barley, wheat, maize, and rice (82–86) and are considered an important target for crop improvement, as they were found to control biotic stress responses and senescence. This large family of plant-specific transcription factors has been named after the first three members characterized: *NO APICAL MERISTEM (NAM), ACTIVATION FACTOR 1* (AF1), and *CUP-SHAPED COTYLEDON 2 (CUC2)*. Besides their role in stress-related pathways, the *NAC* genes are best known for their function in specifying organ boundaries. In Arabidopsis, *CUC1*, *CUC2*, and *CUC3* are expressed in the boundary regions between the SAM and leave primordia and between the IM and FM. Furthermore, they are also found in the regions between different floral organs and in the gynoecium. Multiple *cuc* mutants display organ fusion phenotypes, with different degrees of severity (87–89).

Moving to cereals, only for the maize *NAM1*, *NAM2,* and *NAM3* genes the expression profile was analyzed and resulted to be similar to the profiles of the homologous genes in Arabidopsis (90). Notably, in rice different members of the *NAC* family were shown to be involved in shoot branching and seed size control (91–93).

In Arabidopsis, *CUC* expression is under control of miR164, which is in turn regulated by members of the *TCP* transcription factor family (94,95). It was thus not a surprise to find that also the *TCPs* are among the genes differentially expressed in cereal meristems.

These transcription factors are plant-specific and share a conserved non-canonical basic helix-loop-helix DNA binding domain. *TPC* factors are divided into two classes, according to their sequence homology, and are suggested to work antagonistically to regulate cell proliferation throughout the life cycle of plants.

The maize *BRANCHING ANGLE DEFECTIVE 1 (BAD1)* is one of the few *TCP* transcription factors with a known function in regulating inflorescence architecture. It is expressed in the inflorescence axillary meristems, where it inhibits cell division and proliferation. *bad1* mutants are characterized by an up-right tassel, with acute branching angles (96).

The *TEOSINTE BRANCHED1 (TB1)* allele has been associated with inflorescence development in several crops. *TB1* was selected during maize domestication from teosinte as a major factor involved in axillary branch regulation (97,98). The rice orthologous *OsTB1* or *FINECULM* showed to have a similar function since this

gene is negatively regulating secondary branching (99,100). The orthologous of *TB1* in barley, *INTERMEDIUM*-C (*INT-C/HvTB1*), and wheat *taTB1* were found to be involved in regulating tillering and in determining the fertility of lateral spikelets (101,102).

The last group of cereal-specific TFs is characterized by the presence of the *bHLH* domain, which is composed of 60 aa with DNA-binding and a protein-protein dimerization function. The bHLH superfamily is widespread in the animal and plant kingdom, and its members have been genome-wide identified in several crops (53,103–105), but their role in plant reproductive development is still poorly characterized. In maize, *MALE STERILITY32 (MS32)* was found to be involved in the control of male fertility (106). In the same species, *BARREN STALK1* (BA1) controls the differentiation of the aerial lateral meristems, in connection with auxin signaling (107,108). Also in rice, a member of this family, *LAX PANICLE (LAX1)*, controls axillary meristem formation (109).

PERSPECTIVE

- *Highlight the importance of the field*

Future food security will require improved crops that provide increased grain yield under less favorable environmental conditions. Thanks to the development of high-tech genomics approaches and new breeding technologies, trait development for increased environmental resilience and productivity can count on the discovery of until now unexplored information about genetic variability and gene networks controlling key aspects of plant growth. Plant performance is greatly linked to plant development, which ultimately is decided at the meristematic level. It is then fundamental to comprehend the molecular mechanisms controlling plant meristem identity and the regulation of the meristem transition from indeterminacy to determinacy to further improve yield components as flower, fruit, and seed number.

- *A summary of the current thinking*

One of the possible targets that could help to overcome the plateau in crop yield is the possibility to extend the lifespan of indeterminate meristems, thus allowing the development of more flowers and seeds. Recently extensive molecular and genetic analyses have demonstrated that transcriptional regulators, which are the focus of this review, act as master players regulating discrete developmental programs, enforcing the concept that novel morphological differences may be modulated by changes in the action of these key regulators. Genome sequences, comparative genomics, and functional data are today the tools supporting the identification of molecular hubs at the base of inflorescence differentiation in distantly related species.

- *A comment on future directions*

We are convinced that using genome-wide data analysis for the identification of conserved and cereal-specific potential regulators governing inflorescence architecture, will allow making a careful selection of the best candidates. Further analyses using mutant alleles and/or screening for natural variants, will be required to confirm the role of candidate genes in controlling yield. An extremely powerful method to create novel allelic variation is through the use of genome editing approaches (110,111). CRISP/RCas9 has been used until now mainly to introduce mutations in coding sequences for the generation of null alleles for functional studies (112) but new CRISPR technologies becoming available, like Prime editing (113), which allow also the creation of amino acid substitutions to modulate transcription factor activity or inducing cis-regulatory mutations to inflect gene function by changing the expression profile of a gene.

COMPETING INTERESTS

The authors declare that there are no competing interests associated with the manuscript.

REFERENCES

1.   Prusinkiewicz P, Erasmus Y, Lane B, Harder LD, Coen E. Evolution and development of inflorescence architectures. Science (80-). 2007;316(5830):1452–6.
2.   Somssich M, Je B Il, Simon R, Jackson D. CLAVATA-WUSCHEL signaling in the shoot meristem. Vol. 143, Development (Cambridge). 2016.
3.   Busch W, Miotk A, Ariel FD, Zhao Z, Forner J, Daum G, et al. Transcriptional control of a plant stem cell niche. Dev Cell [Internet]. 2010 May 18 [cited 2020 Feb 28];18(5):841–53. Available from: http://www.ncbi.nlm.nih.gov/pubmed/20493817
4.   Prusinkiewicz P, Erasmus Y, Lane B, Harder LD, Coen E. Evolution and development of inflorescence architectures. Science (80-). 2007 Jun 8;316(5830):1452–6.
5.   Mantegazza O, Gregis V, Chiara M, Selva C, Leo G, Horner DS, et al. Gene coexpression patterns during early development of the native Arabidopsis reproductive meristem: Novel candidate developmental regulators and patterns of functional redundancy. Plant J. 2014;
6.   Digel B, Pankin A, von Korff M. Global transcriptome profiling of developing leaf and shoot apices reveals distinct genetic and environmental control of floral transition and inflorescence development in barley. Plant Cell. 2015;27(9):2318–34.
7.   Eveland AL, Goldshmidt A, Pautler M, Morohashi K, Liseron-Monfils C, Lewis MW, et al. Regulatory modules controlling maize inflorescence architecture. Genome Res. 2014;24(3):431–43.
8.   Feng N, Song G, Guan J, Chen K, Jia M, Huang D, et al. Transcriptome profiling of wheat inflorescence development from spikelet initiation to floral patterning identified stage-specific regulatory Genes. Plant Physiol. 2017;174(3):1779–94.
9.   Harrop TWR, Mantegazza O, Luong AM, Béthune K, Lorieux M, Jouannic S, et al. A set of AP2-like genes is associated with inflorescence branching and architecture in domesticated rice. J Exp Bot. 2019;(July).
10.   Harrop TWR, Din IU, Gregis V, Osnato M, Jouannic S, El Ene Adam H, et al. Gene expression profiling of reproductive meristem types in early rice inflorescences by laser microdissection. 2016;
11.   Leiboff S, Hake S. Reconstructing the Transcriptional Ontogeny of Maize and Sorghum Supports an Inverse Hourglass Model of Inflorescence Development. Curr Biol [Internet]. 2019;29(20):3410-3419.e3. Available from: https://doi.org/10.1016/j.cub.2019.08.044
12.   Lemmon ZH, Park SJ, Jiang K, Van Eck J, Schatz MC, Lippman ZB. The evolution of inflorescence diversity in the nightshades and heterochrony during meristem maturation. Genome Res. 2016;26(12):1676–86.
13.   Liu H, Li G, Yang X, Kuijer HNJ, Liang W, Zhang D. Transcriptome profiling reveals phase-specific gene expression in the developing barley inflorescence. Crop J [Internet]. 2020;8(1):71–86. Available

from: https://doi.org/10.1016/j.cj.2019.04.005

14. Anwar A, Kim JK. Transgenic Breeding Approaches for Improving Abiotic Stress Tolerance: Recent Progress and Future Perspectives. Vol. 21, International journal of molecular sciences. NLM (Medline); 2020.

15. Rabara RC, Tripathi P, Rushton PJ. The potential of transcription factor-based genetic engineering in improving crop tolerance to drought. Vol. 18, OMICS A Journal of Integrative Biology. Mary Ann Liebert Inc.; 2014. p. 601–14.

16. Van Bel M, Diels T, Vancaester E, Kreft L, Botzki A, Van De Peer Y, et al. PLAZA 4.0: An integrative resource for functional, evolutionary and comparative plant genomics. Nucleic Acids Res. 2018;46(D1):D1190–6.

17. Schwarz-Sommer Z, Huijser P, Nacken W, Saedler H, Sommer H. Genetic control of flower development by homeotic genes in Antirrhinum majus. Science (80-). 1990;250(4983):931–6.

18. Arora R, Agarwal P, Ray S, Singh AK, Singh VP, Tyagi AK, et al. MADS-box gene family in rice: Genome-wide identification, organization and expression profiling during reproductive development and stress. BMC Genomics. 2007;8.

19. Parenicová L, de Folter S, Kieffer M, Horner DS, Favalli C, Busscher J, et al. Molecular and Phylogenetic Analyses of the Complete MADS-Box Transcription Factor Family in Arabidopsis: New Openings to the MADS World. Plant Cell. 2003;15:1538–51.

20. Schilling S, Kennedy A, Pan S, Jermiin LS, Melzer R. Genome-wide analysis of MIKC-type MADS-box genes in wheat: pervasive duplications, functional conservation and putative neofunctionalization. New Phytol. 2020;225(1):511–29.

21. Qiong Zhao, Allison L. Weber, Michael D. McMullen, Katherine Guill J, Doebley. MADS-box genes of maize: frequent targets of selection during domestication. Genet Res. 2012;93(1):65–75.

22. Becker A, Theißen G. The major clades of MADS-box genes and their role in the development and evolution of flowering plants. Mol Phylogenet Evol. 2003;29(3):464–89.

23. Callens C, Tucker MR, Zhang D, Wilson ZA. Dissecting the role of MADS-box genes in monocot floral development and diversity. J Exp Bot. 2018;69(10):2435–59.

24. Castelán-Muñoz N, Herrera J, Cajero-Sánchez W, Arrizubieta M, Trejo C, García-Ponce B, et al. MADS-box genes are key components of genetic regulatory networks involved in abiotic stress and plastic developmental responses in plants. Front Plant Sci. 2019;10(July).

25. Schilling S, Pan S, Kennedy A, Melzer R. MADS-box genes and crop domestication: The jack of all traits. J Exp Bot. 2018;69(7):1447–69.

26. Zhao L, Nakazawa M, Takase T, Manabe K, Kobayashi M, Seki M, et al. Overexpression of LSH1, a member of an uncharacterised gene family, causes enhanced light regulation of seedling development. Plant J [Internet]. 2004 Mar [cited 2019 Sep 27];37(5):694–706. Available from: http://www.ncbi.nlm.nih.gov/pubmed/14871309

27. Cho E, Zambryski PC. ORGAN BOUNDARY1 defines a gene expressed at the junction between the shoot apical meristem and lateral organs. Proc Natl Acad Sci U S A. 2011;108(5):2154–9.

28. Takeda S, Hanano K, Kariya A, Shimizu S, Zhao L, Matsui M, et al. CUP-SHAPED COTYLEDON1 transcription factor activates the expression of LSH4 and LSH3, two members of the ALOG gene family, in shoot organ boundary cells. Plant J. 2011;66(6):1066–77.

29. Chen F, Zhou Q, Wu L, Li F, Liu B, Zhang S, et al. Genome-wide identification and characterization of the ALOG gene family in Petunia. BMC Plant Biol. 2019;19(1):1–15.

30. Nan W, Shi S, Jeewani DC, Quan L, Shi X, Wang Z. Genome-Wide Identification and Characterization of wALOG Family Genes Involved in Branch Meristem Development of Branching Head Wheat. Genes (Basel) [Internet]. 2018 Oct 19 [cited 2019 Sep 27];9(10):510. Available from: http://www.ncbi.nlm.nih.gov/pubmed/30347757

31. Yoshida A, Sasao M, Yasuno N, Takagi K, Daimon Y, Chen R, et al. TAWAWA1, a regulator of rice inflorescence architecture, functions through the suppression of meristem phase transition. Proc Natl Acad Sci U S A. 2013;110(2):767–72.

32. Nakano T, Suzuki K, Fujimura T, Shinshi H. Genome-Wide Analysis of the ERF Gene Family in Arabidopsis and Rice. 2006;140:411–32.

33. Rashid M, Guangyuan H, Guangxiao Y, Hussain J, Xu Y. AP2/ERF transcription factor in rice: Genome-wide canvas and syntenic relationships between monocots and eudicots. Evol Bioinforma. 2012;2012(8):321–55.

34. Zhao Y, Ma R, Xu D, Bi H, Xia Z, Peng H. Genome-Wide Identification and Analysis of the AP2

Transcription Factor Gene Family in Wheat (Triticum aestivum L.). Front Plant Sci. 2019;10(October):1–13.

35. Chandler JW. Class VIIIb APETALA2 Ethylene Response Factors in Plant Development. Trends Plant Sci [Internet]. 2018;23(2):151–62. Available from: http://dx.doi.org/10.1016/j.tplants.2017.09.016

36. Chandler JW, Werr W. A phylogenetically conserved APETALA2/ETHYLENE RESPONSE FACTOR, ERF12, regulates Arabidopsis floral development. Plant Mol Biol. 2020;102(1–2):39–54.

37. Chandler JW, Werr W. DORNRÖSCHEN, DORNRÖSCHEN-LIKE, and PUCHI redundantly control floral meristem identity and organ initiation in Arabidopsis. J Exp Bot. 2017;68(13):3457–72.

38. Karim MR, Hirota A, Kwiatkowska D, Tasaka M, Aida M. A role for arabidopsis PUCHI in floral meristem identity and bract suppression. Plant Cell. 2009;21(5):1360–72.

39. Bai X, Huang Y, Mao D, Wen M, Zhang L, Xing Y. Regulatory role of FZP in the determination of panicle branching and spikelet formation in rice. Sci Rep. 2016;6(August 2015):1–11.

40. Zhu QH, Hoque MS, Dennis ES, Upadhyaya NM. Ds tagging of BRANCHED FLORETLESS 1 (BFL1) that mediates the transition from spikelet to floret meristem in rice (Oryza sativa L). BMC Plant Biol. 2003;3:1–13.

41. Komatsu M, Chujo A, Nagato Y, Shimamoto K, Kyozuka J. Frizzy panicle is required to prevent the formation of axillary meristems and to establish floral meristem identity in rice spikelets. Development. 2003;130(16):3841–50.

42. Lee DY, Lee J, Moon S, Park SY, An G. The rice heterochronic gene SUPERNUMERARY BRACT regulates the transition from spikelet meristem to floral meristem. Plant J. 2007;49(1):64–78.

43. Lee DY, An G. Two AP2 family genes, SUPERNUMERARY BRACT (SNB) and OsINDETERMINATE SPIKELET 1 (OsIDS1), synergistically control inflorescence architecture and floral meristem establishment in rice. Plant J. 2012;69(3):445–61.

44. Ren D, Li Y, Zhao F, Sang X, Shi J, Wang N, et al. MULTI-FLORET SPIKELET1, which encodes an AP2/ERF protein, determines spikelet meristem fate and sterile lemma identity in rice. Plant Physiol. 2013;162(2):872–84.

45. Chuck G, Muszynski M, Kellogg E, Hake S, Schmidt RJ. The control of spikelet meristem identity by the branched silkless1 gene in maize. Science (80-). 2002;298(5596):1238–41.

46. Chuck G, Meeley R, Hake S. Floral meristem initiation and meristem cell fate are regulated by the maize AP2 genes ids1 and sid1. Development. 2008;135(18):3013–9.

47. Chuck G, Meeley R, Irish E, Sakai H, Hake S. The maize tasselseed4 microRNA controls sex determination and meristem cell fate by targeting Tasselseed6/indeterminate spikelet1. Nat Genet. 2007;39(12):1517–21.

48. Lee YS, Lee DY, Cho LH, An G. Rice miR172 induces flowering by suppressing OsIDS1 and SNB, two AP2 genes that negatively regulate expression of Ehd1 and florigens. Rice. 2014;7(1):1–13.

49. Debernardi JM, Lin H, Chuck G, Faris JD, Dubcovsky J. microRNA172 plays a crucial role in wheat spike morphogenesis and grain threshability. Dev. 2017;144(11):1966–75.

50. Dobrovolskaya O, Pont C, Sibout R, Martinek P, Badaeva E, Murat F, et al. Frizzy panicle drives supernumerary spikelets in bread wheat. Plant Physiol. 2015;167(1):189–99.

51. Poursarebani N, Seidensticker T, Koppolu R, Trautewig C, Gawroński P, Bini F, et al. The genetic basis of composite spike form in barley and 'miracle-wheat.' Genetics. 2015;201(1):155–65.

52. Simons KJ, Fellers JP, Trick HN, Zhang Z, Tai YS, Gill BS, et al. Molecular characterization of the major wheat domestication gene Q. Genetics. 2006;172(1):547–55.

53. Feller A, MacHemer K, Braun EL, Grotewold E. Evolutionary and comparative analysis of MYB and bHLH plant transcription factors. Plant J. 2011;66(1):94–116.

54. Stracke R, Werber M, Weisshaar B. The R2R3-MYB gene family in Arabidopsis thaliana. Vol. 4, Current Opinion in Plant Biology. Elsevier Ltd; 2001. p. 447–56.

55. Ambawat S, Sharma P, Yadav NR, Yadav RC. MYB transcription factor genes as regulators for plant responses: An overview. Vol. 19, Physiology and Molecular Biology of Plants. Springer; 2013. p. 307–21.

56. Baillo EH, Kimotho RN, Zhang Z, Xu P. Transcription factors associated with abiotic and biotic stress tolerance and their potential for crops improvement. Vol. 10, Genes. MDPI AG; 2019.

57. Chen YH, Cao YY, Wang LJ, Li LM, Yang J, Zou MX. Identification of MYB transcription factor genes and their expression during abiotic stresses in maize. Biol Plant. 2018 Jun 1;62(2):222–30.

58. Dubos C, Stracke R, Grotewold E, Weisshaar B, Martin C, Lepiniec L. MYB transcription factors in

Arabidopsis. Trends Plant Sci. 2010;15(10):573–81.

59. Li C, Ng CKY, Fan LM. MYB transcription factors; active players in abiotic stress signaling. Environ Exp Bot. 2015 Jun 1;114:80–91.

60. Shi Y, Zhao X, Guo S, Dong S, Wen Y, Han Z, et al. ZmCCA1a on Chromosome 10 of Maize Delays Flowering of Arabidopsis thaliana. Front Plant Sci. 2020;11(February):1–15.

61. Zhang L, Liu G, Jia J, Zhao G, Xia C, Zhang L, et al. The wheat MYB-related transcription factor TaMYB72 promotes flowering in rice. J Integr Plant Biol. 2016;58(8):701–4.

62. Ren D, Cui Y, Hu H, Xu Q, Rao Y, Yu X, et al. AH2 encodes a MYB domain protein that determines hull fate and affects grain yield and quality in rice. Plant J. 2019;100(4):813–24.

63. Müller D, Schmitz G, Theres K. Blind homologous R2R3 Myb genes control the pattern of lateral meristem initiation in Arabidopsis. Plant Cell. 2006 Mar 1;18(3):586–97.

64. Vollbrecht E, Springer PS, Goh L, Buckler IV ES, Martienssen R. Architecture of floral branch systems in maize and related grasses. Nature. 2005;436(7054):1119–26.

65. Agarwal P, Arora R, Ray S, Singh AK, Singh VP, Takatsuji H, et al. Genome-wide identification of C2H2 zinc-finger gene family in rice and their phylogeny and expression analysis. Plant Mol Biol. 2007;65(4):467–85.

66. Faraji S, Rasouli SH, Kazemitabar SK. Genome-wide exploration of C2H2 zinc finger family in durum wheat (Triticum turgidum ssp. Durum): insights into the roles in biological processes especially stress response. BioMetals [Internet]. 2018;31(6):1019–42. Available from: https://doi.org/10.1007/s10534-018-0146-y

67. Han G, Lu C, Guo J, Qiao Z, Sui N, Qiu N. C2H2 Zinc Finger Proteins : Master Regulators of Abiotic Stress Responses in Plants. 2020;11(February):1–13.

68. Xiao H, Tang J, Li Y, Wang W, Li X, Jin L, et al. STAMENLESS 1, encoding a single C2H2 zinc finger protein, regulates floral organ identity in rice. Plant J. 2009;59(5):789–801.

69. Huang J, Wang J, Zhang H. Rice ZFP15 gene encoding for a novel C2H2-type zinc finger protein lacking DLN box, is regulated by spike development but not by abiotic stresses. Mol Biol Rep. 2005;32(3):177–83.

70. Li K, Yang J, Liu J, Du X, Wei C, Su W, et al. Cloning, characterization and tissue-specific expression of a cDNA encoding a novel EMBRYONIC FLOWER 2 gene (OsEMF2) in Oryza sativa. DNA Seq - J DNA Seq Mapp. 2006;17(1):74–8.

71. Bakshi M, Oelmüller R. Wrky transcription factors jack of many trades in plants. Plant Signal Behav. 2014;9(FEB):1–18.

72. Gupta S, Mishra VK, Kumari S, Raavi, Chand R, Varadwaj PK. Deciphering genome-wide WRKY gene family of Triticum aestivum L. and their functional role in response to Abiotic stress. Genes and Genomics [Internet]. 2019;41(1):79–94. Available from: http://dx.doi.org/10.1007/s13258-018-0742-9

73. Jiang J, Ma S, Ye N, Jiang M, Cao J, Zhang J. WRKY transcription factors in plant responses to stresses. J Integr Plant Biol. 2017;59(2):86–101.

74. Ning P, Liu C, Kang J, Lv J. Genome-wide analysis of WRKY transcription factors in wheat (Triticum aestivum L.) and differential expression under water deficit condition. PeerJ. 2017;2017(5):1–24.

75. Rushton PJ, Somssich IE, Ringler P, Shen QJ. WRKY transcription factors. Trends Plant Sci [Internet]. 2010;15(5):247–58. Available from: http://dx.doi.org/10.1016/j.tplants.2010.02.006

76. Satapathy L, Kumar D, Kumar M, Mukhopadhyay K. Functional and DNA–protein binding studies of WRKY transcription factors and their expression analysis in response to biotic and abiotic stress in wheat (Triticum aestivum L.). 3 Biotech [Internet]. 2018;8(1). Available from: https://doi.org/10.1007/s13205-017-1064-3

77. Wei KF, Chen J, Chen YF, Wu LJ, Xie DX. Molecular phylogenetic and expression analysis of the complete WRKY transcription factor family in maize. DNA Res. 2012;19(2):153–64.

78. Jang S, Li HY. Overexpression of OsAP2 and OSWRKY24 in arabidopsis results in reduction of plant size. Plant Biotechnol. 2018;35(3):273–9.

79. Qin Z, Lv H, Zhu X, Meng C, Quan T, Wang M, et al. Ectopic Expression of a Wheat WRKY Transcription Factor Gene TaWRKY71-1 Results in Hyponastic Leaves in Arabidopsis thaliana. PLoS One. 2013;8(5).

80. Tian X, Li X, Zhou W, Ren Y, Wang Z, Liu Z, et al. Transcription factor OsWRKY53 positively regulates brassinosteroid signaling and plant architecture. Plant Physiol. 2017;175(3):1337–49.

81. Zhang CQ, Xu Y, Lu Y, Yu HX, Gu MH, Liu QQ. The WRKY transcription factor OsWRKY78 regulates stem elongation and seed development in rice. Planta. 2011;234(3):541–54.

82. Borrill P, Harrington SA, Uauy C. Genome-Wide sequence and expression analysis of the NAC transcription factor family in polyploid wheat. G3 Genes, Genomes, Genet. 2017;7(9):3019–29.

83. Murozuka E, Massange-Sánchez JA, Nielsen K, Gregersen PL, Braumann I. Genome wide characterization of barley NAC transcription factors enables the identification of grain-specific transcription factors exclusive for the Poaceae family of monocotyledonous plants. PLoS One. 2018;13(12):1–28.

84. Nuruzzaman M, Manimekalai R, Sharoni AM, Satoh K, Kondoh H, Ooka H, et al. Genome-wide analysis of NAC transcription factor family in rice. Gene [Internet]. 2010;465(1–2):30–44. Available from: http://dx.doi.org/10.1016/j.gene.2010.06.008

85. Ooka H, Satoh K, Doi K, Nagata T, Otomo Y, Murakami K, et al. Comprehensive Analysis of NAC Family Genes in Oryza sativa and Arabidopsis thaliana. DNA Res. 2003;10(6):239–47.

86. Shiriga K, Sharma R, Kumar K, Yadav SK, Hossain F, Thirunavukkarasu N. Genome-wide identification and expression pattern of drought-responsive members of the NAC family in maize. Meta Gene [Internet]. 2014;2(1):407–17. Available from: http://dx.doi.org/10.1016/j.mgene.2014.05.001

87. Cucinotta M, Manrique S, Cuesta C, Benkova E, Novak O, Colombo L. CUP-SHAPED COTYLEDON1 (CUC1) and CUC2 regulate cytokinin homeostasis to determine ovule number in Arabidopsis. J Exp Bot. 2018;69(21):5169–76.

88. Gonçalves B, Hasson A, Belcram K, Cortizo M, Morin H, Nikovics K, et al. A conserved role for CUP-SHAPED COTYLEDON genes during ovule development. Plant J. 2015;83(4):732–42.

89. Takada S, Hibara KI, Ishida T, Tasaka M. The CUP-SHAPED COTYLEDON1 gene of Arabidopsis regulates shoot apical meristem formation. Development. 2001;128(7):1127–35.

90. Zimmermann R, Werr W. Pattern formation in the monocot embryo as revealed by NAM and CUC3 orthologues from Zea mays L. Plant Mol Biol. 2005;58(5):669–85.

91. Chen X, Lu S, Wang Y, Zhang X, Lv B, Luo L, et al. OsNAC2 encoding a NAC transcription factor that affects plant height through mediating the gibberellic acid pathway in rice. Plant J. 2015;82(2):302–14.

92. Mao C, Ding W, Wu Y, Yu J, He X, Shou H, et al. Overexpression of a NAC-domain protein promotes shoot branching in rice. New Phytol. 2007;176(2):288–98.

93. Mathew IE, Das S, Mahto A, Agarwal P. Three rice NAC transcription factors heteromerize and are associated with seed size. Front Plant Sci. 2016;7(November 2016):1–16.

94. Koyama T, Mitsuda N, Seki M, Shinozaki K, Ohme-Takagi M. TCP transcription factors regulate the activities of ASYMMETRIC LEAVES1 and miR164, as well as the auxin response, during differentiation of leaves in Arabidopsis. Plant Cell. 2010;22(11):3574–88.

95. Uberti-Manassero NG, Lucero LE, Viola IL, Vegetti AC, Gonzalez DH. The class i protein AtTCP15 modulates plant development through a pathway that overlaps with the one affected by CIN-like TCP proteins. J Exp Bot. 2012;63(2):809–23.

96. Bai F, Reinheimer R, Durantini D, Kellogg EA, Schmidt RJ. TCP transcription factor, BRANCH ANGLE DEFECTIVE 1 (BAD1), is required for normal tassel branch angle formation in maize. Proc Natl Acad Sci U S A. 2012;109(30):12225–30.

97. Doebley J, Stec A, Hubbard L. The evolution of apical dominance in maize. Nature. 1997;386(6624):485–8.

98. Hubbard L, Mcsteen P, Doebley J, Hake S. Expression Patterns and Mutant Phenotype of. 2002;1(December):1927–35.

99. Takeda T, Suwa Y, Suzuki M, Kitano H, Ueguchi-Tanaka M, Ashikari M, et al. The OsTB1 gene negatively regulates lateral branching in rice. Plant J. 2003;33(3):513–20.

100. Yano K, Ookawa T, Aya K, Ochiai Y, Hirasawa T, Ebitani T, et al. Isolation of a novel lodging resistance QTL gene involved in strigolactone signaling and its pyramiding with a QTL gene involved in another mechanism. Mol Plant [Internet]. 2015;8(2):303–14. Available from: http://dx.doi.org/10.1016/j.molp.2014.10.009

101. Dixon LE, Greenwood JR, Bencivenga S, Zhang P, Cockram J, Mellers G, et al. TEOSINTE BRANCHED1 regulates inflorescence architecture and development in bread wheat (Triticum aestivum). Plant Cell. 2018;30(3).

102. Ramsay L, Comadran J, Druka A, Marshall DF, Thomas WTB, MacAulay M, et al.

INTERMEDIUM-C, a modifier of lateral spikelet fertility in barley, is an ortholog of the maize domestication gene TEOSINTE BRANCHED 1. Nat Genet. 2011;43(2):169–72.

103. Carretero-Paulet L, Galstyan A, Roig-Villanova I, Martínez-García JF, Bilbao-Castro JR, Robertson DL. Genome-wide classification and evolutionary analysis of the bHLH family of transcription factors in Arabidopsis, poplar, rice, moss, and algae. Plant Physiol. 2010;153(3):1398–412.

104. Li X, Duan X, Jiang H, Sun Y, Tang Y, Yuan Z, et al. Genome-wide analysis of basic/helix-loop-helix transcription factor family in rice and Arabidopsis. Plant Physiol. 2006 Aug;141(4):1167–84.

105. Wei K, Chen H. Comparative functional genomics analysis of bHLH gene family in rice, maize and wheat. BMC Plant Biol. 2018;18(1):1–21.

106. Moon J, Skibbe D, Timofejeva L, Wang CJR, Kelliher T, Kremling K, et al. Regulation of cell divisions and differentiation by MALE STERILITY32 is required for anther development in maize. Plant J. 2013 Nov 5;76(4):592–602.

107. Gallavotti A, Zhao Q, Kyozuka J, Meeley RB, Ritter MK, Doebley JF, et al. The role of barren stalk1 in the architecture of maize. Nature. 2004 Dec 2;432(7017):630–5.

108. Galli M, Gallavotti A. Expanding the Regulatory Network for Meristem Size in Plants. Trends Genet [Internet]. 2016;32(6):372–83. Available from: http://dx.doi.org/10.1016/j.tig.2016.04.001

109. Komatsu K, Maekawa M, Ujiie S, Satake Y, Furutani I, Okamoto H, et al. LAX and SPA: Major regulators of shoot branching in rice. Proc Natl Acad Sci U S A. 2003 Sep 30;100(20):11765–70.

110. Doudna JA, Charpentier E. The new frontier of genome engineering with CRISPR-Cas9. Vol. 346, Science. American Association for the Advancement of Science; 2014.

111. Hsu PD, Lander ES, Zhang F. Development and applications of CRISPR-Cas9 for genome engineering. Vol. 157, Cell. Cell Press; 2014. p. 1262–78.

112. Belhaj K, Chaparro-Garcia A, Kamoun S, Patron NJ, Nekrasov V. Editing plant genomes with CRISPR/Cas9. Vol. 32, Current Opinion in Biotechnology. Elsevier Ltd; 2015. p. 76–84.

113. Anzalone A V., Randolph PB, Davis JR, Sousa AA, Koblan LW, Levy JM, et al. Search-and-replace genome editing without double-strand breaks or donor DNA. Nature. 2019 Dec 5;576(7785):149–57.