Genetic and Molecular Control of Floral Organ Identity in Cereals

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Abstract: Grasses represent a major family of monocots comprising mostly cereals. When compared to their eudicot counterparts, cereals show a remarkable morphological diversity. Understanding the molecular basis of floral organ identity and inflorescence development is crucial to gain insight into the grain development for yield improvement purposes in cereals, however, the exact genetic mechanism of floral organogenesis remains elusive due to their complex inflorescence architecture. Extensive molecular analyses of Arabidopsis and other plant genera and species have established the ABCDE floral organ identity model. According to this model, hierarchical combinatorial activities of A, B, C, D, and E classes of homeotic genes regulate the identity of different floral organs with partial conservation and partial diversification between eudicots and cereals. Here, we review the developmental role of A, B, C, D, and E gene classes and explore the recent advances in understanding the floral development and subsequent organ specification in major cereals with reference to model plants. Furthermore, we discuss the evolutionary relationships among known floral organ identity genes. This comparative overview of floral developmental genes and associated regulatory factors, within and between species, will provide a thorough understanding of underlying complex genetic and molecular control of flower development and floral organ identity, which can be helpful to devise innovative strategies for grain yield improvement in cereals.

Keywords: ABCDE model; cereals; evolutionary relationships; flower organ identity; floral speciation; MADS-box genes

1. Introduction

Cereals are clearly critical for global food security. They provide approximately 60% of human caloric requirement and this figure can even exceed 80% in resource-poor countries [1]. However, the exponential increase in the world population, soaring food prices and constant depletion of arable land resources due to climate change have made it inevitable to develop cereal crops with increased grain yield [2]. Cereals belong to the grass family Poaceae, which is one of the largest groups of
monocotyledonous plants, with almost 12,000 species [3]. The grass family is monophyletic and diverged from eudicots approximately 125–150 million years ago [4,5]. Grasses show remarkable diversity in overall plant morphology, physiology, genetics, and ecology compared to their eudicot counterparts [6]. For example, spikelets are characteristic structural units of grass inflorescence, which (depending upon species) show determinate or indeterminate growth. Spikelets are composed of one to several florets but unlike eudicot flowers, these florets possess bract-like structures called lemma, palea, and lodicules, instead of sepals and petals [7,8].

The Poaceae family has two important model crop species; rice (Oryza sativa) and maize (Zea mays). Each has been used to study flower development processes at the molecular level. The genome of rice is exceptionally small compared to other grass species and has been fully sequenced [9,10]. In addition, the rice genome is conducive for effective positional cloning and genetic transformation; making it ideal for developmental biology studies [11–13]. Similarly, the genome of maize has also been fully sequenced [14], is amenable to positional cloning, and the species has simple reproductive biology [7,15]. Both of these species show synteny [9], thus the progress in one species has been facilitating the progress in the other species.

In addition to rice and maize, the Poaceae family also contains Brachypodium distachyon, a promising model plant that is anatomically similar to the majority of forage grasses and temperate cereals including wheat (Triticum aestivum), the “king of cereals”. B. distachyon has a short life cycle and is readily cultivatable. The genome of B. distachyon has already been sequenced [16] and it offers a highly efficient genetic transformation system. These qualities make B. distachyon suitable for functional genomic studies of grass related traits [17–19]. In comparison, wheat is the most important staple crop in temperate zones and a major source of starch, energy and dietary fiber. As an example, bread wheat alone provides 20% of the daily calorie intake in the UK [20]. However, wheat functional genomic studies were limited due to the lack of a quality reference genome sequence and hexaploid nature of the species [21,22]. More recently, a high quality, fully annotated reference genome of hexaploid wheat has been delivered which can accelerate research in wheat developmental biology and genomics assisted breeding [23]. In recent years, significant progress has been made towards understanding the genetic regulation of spike development in Brachypodium, wheat, and barley [24–31]. These studies revealed striking similarities between Brachypodium, wheat, and barley, with highly conserved genetic regulation of inflorescence development in these species. Thus, understanding the molecular control of inflorescence development and floral organ identity in model species will expand our knowledge about the genetic architecture of the spike development in all economically important grasses.

Floral organs control grain development. Previously, a simple yet elegant ABC model of floral organ identity was devised to demonstrate the molecular control of floral development in model plants [32]. This model proposed that combinatorial activities of three homeotic gene classes specify four floral organs i.e., sepal, petal, stamen, and carpel. Class A genes, when expressed alone, produce sepals. The expression of classes A and B together directs petal identity. The expression of classes B and C together regulates stamen identity and the expression of Class C genes alone determines carpel identity. Subsequently, two other floral identity gene classes were identified. Class D genes in Petunia [33] and the redundant class E genes (SEPI–4) in Arabidopsis [34,35]. The current model consists of these five classes of floral-homeotic, MADS-box genes (A, B, C, D, and E). The hierarchical combination of these five gene classes thus determines floral organ identity [36].

In higher model plants, especially Arabidopsis and rice, the ABCDE model has helped explain the molecular control of floral organ identity to some extent. This is largely due to their relatively small genome size and the extensive research associated with each of these model species. Analyses of the floral homeotic genes of these species suggest that the same flower organ identity model can be applied to other cereals [37], including Brachypodium, maize, and wheat. This review explores recent advances in rice, maize, Brachypodium, and wheat floral development and subsequent organ specification, with reference to the model plant Arabidopsis. Plethora of studies revealed novel regulatory factors and pathways that contribute to the unique morphology of the grasses. However, the vast array of
functions performed by floral homeotic genes and the large body of literature devoted to this subject makes it difficult to comprehensively review all aspects of the genetic control of floral development. Here, we tried to review the comparisons of floral development genes, within and between species that will expand our understanding of the complex molecular genetic control of floral development and flower organ identity especially in grasses.

2. Inflorescence Morphology and Development

The grass family includes several agriculturally and economically important species including rice, wheat, maize, sorghum, and barley. Developmental and genetic pathways controlling the shape of inflorescence architecture and development in these important crops have been reviewed briefly [27,28,38–40]. All grass inflorescences have a characteristic basal structural unit, the spikelet, composed of one to several florets depending upon the species [6]. These florets are surrounded by bract-like structures known as glumes. Most grass species possess unique inflorescence organization and structure distinct from eudicots and even from other monocots [41]. For example, Arabidopsis bears indeterminate inflorescence with several branched flowers. The grasses like Brachypodium, Hordeum, Secale, and Triticum inflorescences carry sessile spikelets on the rachis. In contrast, Avena, Echinochloa, Oryza, Panicum, Setaria, and Sorghum bear long branched inflorescence where spikelets are pedunculate [42] (Figure 1A). Moreover, the Arabidopsis inflorescence meristem normally differentiates only into branch meristem and floral meristem whereas several specialized axillary meristems are formed in grass spikes [40] (Figure 1B). Unlike their eudicot counterparts, the grass florets possess bract-like structures; lemma, palea, and lodicules in place of sepals and petals [8].

Among cereals, rice exhibits distinct inflorescence morphology compared to that of Brachypodium and wheat [24,38,40,43]. The spikelet is the basal structural unit in these three grass species. The rice inflorescence is relatively complex and comprised of long stalked panicles in which primary branches are directly attached to the main axis (rachis) that further produce secondary branches, lateral spikelets and terminal spikelets [38]. By contrast, there exists only one rachis in Brachypodium and wheat that directly bears the spikelets in an alternating configuration [24,28]. Spikelets in these species also bear rudimentary glumes and floret primordia. In rice, the single spikelet can produce only a single floret [44], whereas the wheat spikelet contains several florets and normally four or five of these reach anthesis [45]. Unlike wheat and rice, the inflorescence of Brachypodium carries only two or three lateral spikelets and a single terminal spikelet [24]. Each spikelet contains ~11 florets, arranged in a distichous phyllotaxy around central axis. Overall, the organization and structure of floral organs are conserved among rice, Brachypodium, and wheat, with the exception of three additional stamens within a floret in rice [24,28,38] (Figure 1C). The grass floret contains lemma, palea, lodicules, stamens, and pistils. The pistil is comprised of three fused carpels which surround a single ovule. The apical region of the pistil bifurcates with feathery stigmas. Morphological analysis suggested that lodicules are homologues of petals [46], which together with the lemma and palea are unique to grasses.

Inflorescence development is regulated by several types of meristems [44,47] and starts with the transition of the shoot apical meristem (SAM) into an inflorescence meristem (IM). In Brachypodium and wheat, the IM directly generates the spikelet meristem (SM) [24,28,43], while in rice the IM generates the primary branch meristem (pBM) followed by the secondary branch meristem (sBM) which then finally configure the spikelet meristems (SMs) [40] (Figure 1B). The SMs generate floral meristems (FMs), which subsequently determine floral organ identity. All grasses show indeterminate growth starting from SAM to just before SM determinacy. However, the SM to FM transition is determinate and critical [48] as it is the final phase at which the meristem activity stops. By this stage, stem cells are believed to exhaust all their energy due to continuous formation of floral organs and floret primordia [47].
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Figure 1. Graphical representation of inflorescences, phase transition and transverse flowers. (A) Structural configuration of inflorescence in Arabidopsis, rice, maize, Brachypodium and wheat. Color codes. Green line: rachis; yellow line: primary branch; blue line: secondary branch; green circles: spikelet/spikelet pair meristems; maroon circle/oval: terminal spikelet; orange circle: floral meristems. (B) Regulation of meristem transition in Arabidopsis, rice, maize, Brachypodium, and wheat. Green arrow: multiple meristems formation; blue arrow: single meristem formation; orange dashed arrow: abortion of floral meristems. (C) Schematic representation of transverse spikelet/flower. Color codes: Blue: palea; dark orange: lemma; gold: lodicules; green: sepal; green circle: rachis; gray: glume; pink: pistil; red: petal; yellow: stamen. Abbreviations: BR: branch; BM: branch meristem; FM: floral meristem; GL: glume; IM: inflorescence meristem; LE: lemma; LO: lodicule; LS: lateral spikelet; LSM: lateral spikelet meristem; PA: palea; PB: primary branch; PE: petal; Pi: pistil; PBM: primary branch meristem; RA: rachis; Ra: rachilla; SB: secondary branch; SE: sepal; SBM: secondary branch meristem; SM: spikelet meristem; SPM: spikelet pair meristem; ST: stamen; TS: terminal spikelet.

In contrast to Brachypodium, wheat, and rice, maize is a monoecious crop in which male and female organs occur separately on the same plant. The male inflorescence at the shoot apex is known as tassel that bears paired spikelets while the female inflorescence occurs in the leaf axil which is termed as ear [40]. Male IM produce long indeterminate branches which further differentiate into short secondary branches that bear spikelet pair meristems (SPMs). Each SPM initiate two SMs, which in turn produce two FMs each (Figure 1B). The female inflorescence (ear) is produced on the main stalk, hence SPMs are directly attached to the main stem. SPMs are transient and bear a pair of SMs. SMs are also transient which in turn produce two FMs. Each spikelet bears two staminate flowers called florets and only one of these florets produces a fertile flower. Flowers further develop into different floral organs such as lemma, palea, lodicules, stamens, and carpels. Apart from shapes and
position of male and female inflorescences, the arrest of stamen formation in ear florets and of pistil formation in tassel florets makes it easy to distinguish male and female inflorescences [49]. Over the last two decades, several genetic factors involved in flower development have been identified which mainly function as trans-regulatory elements. Here, we will discuss the latest knowledge about the association of MADS-box- and non-MADS-box-related gene families with inflorescence development and floral organ identity in grasses.

3. Role of MADS-Box Transcription Factors in Floral Organ Identity

MADS-box transcription factors are involved in various biological processes and have been identified in almost all groups of eukaryotes. The name MADS was derived from combining the names of MINICHROMOSOME MAINTENANCE 1 of Saccharomyces cerevisiae, AGAMOUS of Arabidopsis thaliana, DEFICIENS of Antirrhinum majus, and SERUM RESPONSE FACTOR of Homo sapiens [50]. All MADS-box TFs have a highly conserved ~60 amino acids long DNA binding MADS domain at the N-terminal region which binds to CArG boxes on DNA [51]. Flowering plant genomes contain approximately 100 MADS-box genes, which are further categorized into M-type and MIKC-type MADS genes [52]. Only a few M-type MADS are functionally characterized so far [53], however, plant MIKC-type MADS-box genes have been extensively studied [54]. In plants, the diversification of MADS-box genes is closely linked to the evolution of important organs, such as seeds, flowers, and fruits [55]. Moreover, morphological variations in inflorescence of grass family are closely associated with changes in copy number, expression patterns, and interactions between MIKC-type MADS-box genes [56]. In flowering plants, combinatorial activities of the five classes of MIKC-type MADS-domain genes define floral organ identity. According to the Arabidopsis “floral quartet model”, sepals are specified by class A and E genes in the first whorl; petals by class A, B, and E genes in the second whorl; stamens by class B, C, and E genes in the third whorl; and carpels by class C, and E genes in the fourth whorl [54]. The ovule identity gene FLORAL BINDING PROTEIN 11 (FBP11) was first identified and functionally characterized in Petunia and classified as D class gene [33]. In Arabidopsis, ovule identity is controlled by AGAMOUS subfamily member SEEDSTICK (STK) [57]. Functional divergence, duplication, and evolutionary relationships among these five classes of homeotic genes, identified in Arabidopsis and major cereals, are summarized in Table 1. Modified ABCDE models showing the complex genetic interaction of MADS-box TFs’ and other important regulators in Arabidopsis and cereals are illustrated in Figure 2.
Table 1. Genes controlling floral organ identity in cereals.

| Arabidopsis Gene | Subfamily | Class | Putative Role | Rice | Maize | Wheat | Brachypodium | References |
|------------------|-----------|-------|---------------|------|-------|--------|--------------|------------|
| AP1              | AP1       | A     | Promote floral meristems, sepals, petals or lemma/palea identities | OsMADS14, 15 | ZMM4, 15 | WFUL1, TaAGL25 | BrMADS33 | [31,58–66] |
|                  |           |       |               | OsMADS15 | ZAP1   | WFUL2  | BrMADS10    |            |
|                  |           |       |               | OsMADS18 | -      | WFUL3, TaAGL10 | BrMADS3 |            |
|                  |           |       |               | OsMADS20 | -      | -      | BrMADS31    |            |
| AP2              | AP2       | A     | Spikelet/floral meristem identity and lodicule identity | IDS1, SNB | ids1, sid1 | TaAP2 | -            | [24,25,67–75] |
|                  |           |       |               | MFS1   | MFS1   | TaQ    | -            |            |
|                  |           |       |               | EZP    | EZP    | WFZP   | -            |            |
|                  |           |       |               | BD1    | BD1    | -      | MOS1         |            |
| AP3              | AP3       | B     | Lodicule and stamen identity | OsMADS16/SPW1 | Silky1 | WAP3 | BrMADS5 |            |
|                  |           |       |               | OsMADS2 | ZMM16  | WPI2   | BrMADS20 |            |
|                  |           |       |               | OsMADS4 | ZMM18, 29 | WP11 | BrMADS16 |            |
| PI               | PI        | B     | Integuments and seed development | OsMADS29, 30 | ZMM17 | WBP, TaAGL35 | BrMADS17, 23, 38 | [31,84,87–91] |
| ABSTT16, GOA     | B$_{nister}$ | -     | Stamen and carpel identity | OsMADS3 | ZMM2 | WAG-2 | BrMADS14 | [31,57,92–98] |
| AG, SHP1, SHP2   | AG       | C     | Ovule identity | OsMADS13 | ZMM1, ZAG2 | WSTK, TaAGL9, 31 | BrMADS2 | [30,31,57,62,90,99–103] |
| STK              | AG       | D     | FM determinacy and floral organ identity | OsMADS21 | - | - | BrMADS4 |            |
| SEP (1-4)        | SEP      | E     | FM determinacy and floral organ identity | OsMADS7/45 | ZMM6 | WSEP, TaAGL16, 28,30 | BrMADS26 | [31,34,104–108] |
| -                | LOFSEP   | E     | Stamen and carpel identity | OsMADS824 | ZMM7/27 | TaMADS1 | BrMADS32 |            |
| -                | AGL6     | E     | Ovule identity | OsMADS34 | ZMM8/14 | WLS1, TaAGL24 | BrMADS11 | [31,104,107,109–112] |
| -                |          |       |               | OsMADS34 | - | TaAGL3, 5, 8, 34, 40 | BrMADS7 |            |
| -                |          |       |               | OsMADS34/PAP2 | ZMM24, 31 | TaAGL27 | BrMADS1 |            |
| CRC              | YABBY-like | -     | Carpel identity | DL | Dr1, 2 | TaDL | -            | [77,80,118–120] |
| UFO              | F-box    | -     | Positive regulation of B & C class MADS | APO1 | - | - | - | [121–123] |
| -                | DoF      | -     | Lemma and Palea identity? | CFO1, G1/ELE, id-1 | - | - | - | [124–126] |
Figure 2. ABCDE models of floral organ identity. Revised floral organ identity models in Arabidopsis, rice, maize, Brachypodium, and wheat. Class (A)-genes indicated in green, class B in red, class C in dark blue, class D in light blue, class E yellow, and non-MADS in purple. Solid colors show functional data, color gradients represent expression analysis data, while color patterns indicate hypothesized functions. Antagonistic interactions are indicated with barred lines, black arrows illustrate positive regulation of the corresponding genes, and a comma symbolizes duplicated gene interaction. Abbreviations: CA: Carpel; LO: Lodicule; OV: Ovule; PA: Palea; PE: Petal; SE: Sepal; ST: Stamen. For gene abbreviations see text.

3.1. Class A Homeotic Genes

In Arabidopsis, class A genes include APETALA 1 and 2 (AP1 and AP2), of which only AP1 encodes a MADS-box TF. AP1 is expressed only in sepals and petals (two outer whorls) and has an additional role in floral meristem determinacy [61]. Similar expression and functional patterns have been reported in Antirrhinum class-(A) ortholog [127]. In eudicots, class (A)-functions are defined by AP1, CAULIFLOWER (CAL), and FRUITFULL (FUL) genes, whereas in monocots only FUL-like genes are present which are associated with class (A)-function [128]. Recently, Wu et al. [65] demonstrated that grass-specific FUL-like genes are required to specify palea and lodicule identities in addition to their function of specifying meristem identity. Similar results were reported for rice and wheat, wherein AP1 clade genes together with class E SEPALLATA (SEP) genes were shown to participate in the transition from SAM to IM [112,129].
The API homologs identified in rice include OsMADS14, OsMADS15, OsMADS18, and OsMADS20, all of which belong to the FRUITFULL (FUL) lineage [59]. Ectopic expression of OsMADS14 in rice suggests its involvement in floral meristem control to promote flowering. On the other hand, loss-of-function loss-of-function mutations in Osmads15 indicate the role of API in palea formation with no effect on lodicule development [130]. A more recent study in rice employing both single and double mutants of OsMADS14 and Osmads15 [65] provided strong evidence that rice API/FUL-like genes are essential for specifying lemma/palea and lodicule identities during the floral development process. Because lemma and palea are considered homologous structures to sepals and petals of eudicots, respectively, therefore, it is possible that API/FUL-like genes are independently recruited to fulfill the function of class A genes in grass species. Maize orthologs of API include Zea mays APETALA1 (ZAP1), Zea mays MADS4, and 15 (ZMM4, ZMM15) [62]. Phylogenetic analysis showed that ZAP1 is an ortholog of OsMADS15 [131]. Northern blot analysis demonstrated that ZAP1 was expressed in the lemma/palea and lodicules, but not in stamens and pistils [62]. These results suggest that ZAP1 is a putative class-(A) gene with a possible repressive interaction with class C genes. ZMM4 and ZMM15 are orthologs of OsMADS14 and ZMM4 and have been reported to be involved in inflorescence development and floral induction [58], which is consistent with the function of API homologs from Arabidopsis and rice.

The Brachypodium genome contains at least four (A)-class genes, BdMADS3, 10, 31, and 33, which are orthologs of OsMADS18, OsMADS15, OsMADS20, and OsMADS14, respectively. BdMADS3, 10, and 33 were observed to be strongly expressed in the lemma and palea, but not in lodicules and stamens with the exception of BdMADS3 that also strongly expressed in stamens [31]. BdMADS31 was absent in all floral organs but was weakly expressed in leaves similar to the expression pattern of Arabidopsis and rice orthologs [132,133]. These expression pattern studies suggest the involvement of BdMADS3, 10, and 33 in (A)-class performance; however, further functional analyses are required to confirm their regulatory roles in floral organ identity.

Wheat has five FUL-like paralogs including WFUL1/VERNALIZATION1 (VRN1), WFUL2, WFUL3, TaAGL10, and TaAGL25 [117,128]. Phylogenetic analysis showed that these are the orthologs of OsMADS14, OsMADS15, and OsMADS18 [60], an observation consistent with the current phylogenetic tree (Figure 3). Previously it was thought that WFUL1 had no (A)-class function and was only involved in the transition from the vegetative to reproductive phase [63,134], but recent studies suggest that VRN1/WFUL1 is expressed in leaves and the shoot apex, where it is required for the long-day flowering response and inflorescence meristem identity [64,134,135]. ODDSOC2 is a MADS-box TF and downstream target of VRN1 that functions to repress flowering and has been observed to be downregulated in plants with active VRN1 alleles and vernalization [136]. Another study reported that WFUL1 and WFUL3 are expressed in all floral organs with limited or no expression of WFUL2 in stamens and pistils [60], suggesting that WFUL2 has diversified functions in outer (palea and lodicule) and inner (stamen and pistil) floral whors. Yeast two-hybrid and yeast three-hybrid analyses demonstrated that WFUL2 interacts with the B and E classes of MADS-box genes [60]. These findings in combination with the expression pattern analysis illustrate that WFUL2 has a major role in lemma/palea and lodicule identities in wheat florets. It is noteworthy that WFUL1/VRN1 has a more important role in leaf development indicating functional diversification between wheat FUL-like genes. Similarly, functional diversification between rice FUL1 (OsMADS14) and FUL2 (OsMADS15) has been observed. Single mutant of OsMADS14 showed lower seed setting, but no floret-specific mutant phenotype could be observed when grown under natural field conditions. However, under greenhouse conditions the mutant plants had small paleae and showed the homeotic transformation from lodicules to stamen-like organs. Whereas paddy field-grown osmads15 plants showed 45% smaller paleae, without affecting the organ identity. However, greenhouse-grown osmads15 plants had elongated empty glumes and 100% reduced paleae. Additionally, osmads15 plants showed no homeotic transformation of inner three floral organs under both growing conditions [65].
All angiosperms contain AP2 TFs, which, in addition to their role in the regulation of floral development, are implicated in primary and secondary metabolism, growth and development, and response to stress [140]. In Arabidopsis, AP2 is required for the establishment of floral meristems, floral organ identity, and regulation of floral homeotic gene expression [70]. In rice, two AP2-like genes—INDETERMINATE SPIKELET1 (IDS1) and SUPERNUMERARY BRACT (SNB)—synergistically control lodicule development [72]. Another AP2-like gene, named FRIZZLE PANICLE (FZP), prevents the formation of axillary meristem in rice but controls the spikelet meristem identity [71]. FZP has also been observed to regulate the transition from panicle branching to spikelet formation in rice by repressing RICE FLORICAULA LEAFY (RFL)/ABERRANT PANICLE ORGANIZATION2 (APO2). In addition, FZP overexpression positively regulate B and E class MADS-box genes in floral meristem suggesting its role in floral organ identity [67]. MULTI-FLORET SPIKELET1 (MFS1) is another AP2-type gene that positively regulates rice IDS1 and SNB genes [74]. Rice IDS1 and SNB regulate the transition from spikelet meristem to floral meristem [141]. Both of these genes display strong functional resemblance to maize indeterminate spikelet1 (ids1) and sister of indeterminate spikelet1 (sid1), respectively, which are also required to initiate floral meristems and to control spikelet meristem determinacy [68]. Similar to the function of AP2 in Arabidopsis, ids1 and sid1 negatively regulate class C gene function within the lateral organs of the spikelet. Likewise, maize BRANCHED SILKLESS1
(BD1) encodes an ethylene responsive factor (ERF/AP2) that regulates the spikelet meristem identity and mutation in BD1 produces indeterminate floral branching [69]. Like rice FZP and maize BD1, Brachypodium MORE SPIKELETS1 (MOS1) determines spikelet meristem identity as the mos1 mutant showed increased number of axillary meristems compared with the wild type [24]. In wheat, Wheat FZP (WFZP) controls spikelet meristem identity that drives the formation of supernumerary spikelets by repressing meristem formation and differentiation [25]. The regulation of spikelet meristem identity by AP2-like genes in rice, maize, Brachypodium, and wheat indicates that their function is conserved among distantly related grass species including agriculturally important crops. In addition, wheat genome also contain TaQ and TaAP2. The wheat domestication gene (TaQ) has a role in inflorescence shape, glume shape, glume tenacity, and spike length [27,75]. Phylogenetic analysis and transcriptional pattern of wheat TaAP2 revealed its orthologous relationship with barley HvAP2/Cly1, which is involved in lodicule identity [73,142]. This observation demonstrates that like rice AP2-like orthologs, wheat TaAP2 might also associated with lodicule identity [72,74], suggesting their functional similarities in grasses.

In recent years, evolutionary conserved micro-RNAs (miRNAs) have been identified and played a crucial role in plant organogenesis. miR172 appears with the evolution in angiosperms and has been identified in Arabidopsis, rice, maize, barley, and wheat. The level of miR172 increases with plant age and its expression is under photoperiodic control [143]. It is an active repressor of all AP2-like TFs, which are thought to participate in floral patterning. AP2 has been demonstrated to bind and repress the expression of miR172b [144]. Early studies reported AP2 transcripts in all floral organs [70], however recent observations show that AP2 expression is restricted to sepals and petals compared to that of miR172 that predominantly expressed in inner floral whorls (stamen, carpel, and ovule) [145]. These findings suggest an antagonistic interaction of AP2 and miR172 in plant developmental transitions.

In cereals, functionally characterized targets of miR172 include Zea mays indeterminate spikelet1 (ids1) and sister of indeterminate spikelet1 (sid1) [68], Oryza sativa SUPERNUMERARY BRACT (OsSNB) [146], and Hordeum vulgare Cleistogamy1 (Cly1) [142]. Wheat domestication gene TaQ is also a target of miR172, however it is not clear if miR172 mediated regulation has a role in domestication [147]. These investigations provide new insights into the ancient role of miRNAs about floral organ regulation in cereals.

3.2. Class B Homeotic Genes

Arabidopsis class B homeotic genes include AP3 and PISTILLATA (PI) that are required for petal and stamen identities. Single mutants of these genes caused conversion of petals to sepals in the second floral whorl and stamens to carpels in the third floral whorl [78,81]. Rice has two orthologs of PI: OsMADS2 and OsMADS4 [148]. RNAi suppression of OsMADS2 showed homeotic changes in lodicules with no effect on stamens [83], whereas RNAi suppression of OsMADS4 showed no alteration in these floral organs [86]. Interestingly, simultaneous mutations in both genes caused the conversion of lodicules and stamens into palea and carpel-like structures respectively. These observations suggest an equal role for both genes in stamen development, with OsMADS2 more important in lodicule identity. Similarly, maize contains three orthologs of Arabidopsis PI; Zea mays MAD16, 18, and 29 (ZMM16, ZMM18, and ZMM29). Mutation in ZMM16 produced a Sterile Tassel Silky Ear1 (STSI) phenotype in which lodicules transformed into palea-like and stamens into carpel-like structures [85]. Phylogenetic analysis showed that ZMM16 as an ortholog of OsMADS2 while ZMM18 and ZMM29 are orthologous to OsMADS4. Recently, a study reported that ZMM16/STSI (together with its paralogs ZMM18 and ZMM29) forms obligate heterodimers with maize SILKY1 (SI1) and specifies organ identity in second and third floral whorls [149]. Interestingly, RNAi knockdowns of ZMM18 and ZMM29 showed no detectable floret phenotype, indicating that STSI can compensate ZMM18/29 reduction, but ZMM18/29 cannot compensate for STSI reduction. With this evidence, it is possible to speculate a role for maize AP3/PI-like genes.
The sole ortholog of AP3 in rice; OsMADS16/SUPERWOMAN1 (SPW1) has been observed to interact with rice PI-like genes. OsMADS16 knockdown mutant showed homeotic conversion of lodicules and stamens to palea and carpel-like structures, respectively, similar to PI-types [80]. Similarly, the loss-of-function mutant of maize SILKY1 (AP3 ortholog) showed alterations in lodicules and stamens [76]. As lodicules represent second whorl (petals), their transformation into palea-like structures support the hypothesis that petals of eudicots are likely to be modified into lodicules in grasses. Furthermore, Arabidopsis and maize class B genes showed similar biochemical activities in vivo and in vitro [85]. Collectively, these findings suggest that the function of class B genes is somewhat conserved between grasses and eudicots.

The Brachypodium genome contains three B class genes: BdMADS5, 16, and 20. BdMADS5 is an ortholog of Arabidopsis AP3 and rice OsMADS16. Similarly, BdMADS16 and BdMADS20 are orthologs of OsMADS4 and OsMADS2, respectively, and are clustered with Arabidopsis PI [31]. Strong expression of Brachypodium B class genes was detected in lodicules and stamens, with BdMADS16 expressed in carpels as well. However, transcript abundance of all B class genes was very low in the lemma and palea in Brachypodium similar to those of Arabidopsis and rice B class genes [132,133]. Although their expression patterns suggest that BdMADS5, 16, and 20 have conserved roles in lodicule and stamen identity, functional analyses of these genes remain to be conducted to confirm these hypotheses.

WAP3, also called TaAP3 is a wheat ortholog of Arabidopsis AP3, which is encoded by two highly homologous genes: TaMADS#51 and TaMADS#82 [82,131]. Northern blot analysis revealed that WAP3 expression was restricted to young spikes during floral development and possibly associated with the induction of pistillody (homeotic conversion of stamens into carpel-like structures) [79]. WAP3 is also involved in the homeotic transformation of lodicules and stamens into palea and pistil-like structures, respectively [77]. Wheat genome also contains two PI-like genes: WPI1 and WPI2. Phylogenetic analysis revealed close orthologous relationships of WPI1 with OsMADS4, and that of WPI2 with OsMADS2. Similar to WAP3, wheat PI-type genes were reported to be involved in lodicule and stamen development and their homeotic transformation into palea and pistil-like structures. Hama et al. [77] reported that WAP3 and WPI were highly expressed in the primordia of lodicules and stamens. Low expression patterns of wheat B class genes were detected in pistil-like stamens of an alloplasmic wheat line having the Aegilops crassa Boiss. cytoplasm and lacking the Rfd1 gene, indicating that these genes gradually disappear from the fourth whorl (carpel/pistil) just like Arabidopsis PI [81]. These observations strongly suggest that wheat class B genes are associated with the induction of pistillody, a direct consequence of changes in copy number and expression of WAP3 and WPI’s in third and fourth whorls confirming that WAP3 and WPI’s exhibit class B functions.

BSISTER genes, closely related to class B MADS-box genes, have been identified through phylogenetic studies. Members of this subfamily regulate female reproductive organs and seed development [150]. All BSISTER MADS-box genes investigated to date are expressed during early ovule development indicating that these genes may be required for ovule identity. Arabidopsis has two BSISTER genes—ARABIDOPSIS BSISTER (ABS)/TRANSPARENT TESTA16 (TT16) and GORDITA (GOA)—both expressed in mature ovules [88,89]. Yang et al. [91] has functionally characterized the rice BSISTER MADS-box gene; OsMADS29. His findings demonstrate that OsMADS29 expressed only in floral but not vegetative organs. Another study involving RT-PCR revealed that OsMADS29 expressed in ovules, consistent with previously reported patterns for wheat BSISTER (WBsis) and maize ZMM17 [87,90]. However, knock-down of OsMADS29 by double-stranded RNA-mediated interference (RNAi) resulted in shrunved and/or aborted seeds [91], suggesting that OsMADS29 also has important functions in seed development of rice by regulating cell degeneration of maternal tissues. Furthermore, Arabidopsis and rice BSISTER and D-class genes show overlapping expression patterns [151]. More recently, Schilling et al. [84] investigated another BSISTER gene (OsMADS30) in rice. This gene was weakly expressed in ovules. Further, the plants carrying a T-DNA insertion in OsMADS30 showed no aberrant phenotype, indicating that this gene is either not required for ovule specification or its function is obscured by another class D gene (OsMADS21). Brachypodium also
contains three BSISTER genes: BdMADS17, 23, and 38. Weak expression of BdMADS17 and BdMADS23 was detected in palea but absent in ovules. However, BdMADS38 was weakly expressed in stamens only [31]. Altogether, these results suggest that BSISTER genes do not possess a strict function, instead of play overlapping roles in whole reproductive ontogeny.

3.3. Class C and D homeotic genes

It is believed that during the divergence of angiosperm and gymnosperm lineages, an ancient duplication resulted in the class C origin, including all stamen and carpel identity genes and class D or ovule specification genes [98,99,152]. This type of classification is reported in several phylogenetic studies [30,31,131,153], and has therefore been adopted in this review. Arabidopsis has three class C homeotic genes: AGAMOUS (AG) and SHATTERPROOF1 and 2 (SHP1 and SHP2). Arabidopsis typical class C gene AG specifies stamen (third whorl) and carpel (fourth whorl) identities and has an additional role in floral meristem determinacy [93]. In the absence of AG activity, class (A)-gene function expands to the 3rd and 4th whorls [32,154], which suggests antagonistic interaction between these two classes of homeotic genes. The additional C class genes of Arabidopsis, SHPI and SHP2, are required for carpel and fruit dehiscence zone specifications [57,155]. Like grass class B genes, the function of class C genes are also diversified in grasses due to events of duplication and subfunctionalization of these genes during evolution. Rice has two duplicated class C genes; OsMADS3 and OsMADS58. Yamaguchi et al. [98] investigated single mutants of rice class C genes and reported interaction with the class D gene OsMADS13, regulating floral meristem determinacy with redundant mediation of class C gene functions. Mutant and transgenic analyses showed that OsMADS58 regulates floral determinacy with minor effects on carpel identity, while OsMADS3 predominately regulates stamen identity and prevents lodicule development with minor effects on floral determinacy. As floral determinacy is defined by class (A)-genes, OsMADS58 probably has reduced AG activity in the third and fourth whorls compared to OsMADS3. Furthermore, the rice class B gene OsMADS16 interacts with class C genes to suppress indeterminate growth within floral meristems [156]. These findings indicate that class C genes play a dominant role in stamen and carpel identity, with a minor role in floral meristem determinacy and possible antagonistic interaction between A and C class genes. A study conducted by Dreni et al. [92] demonstrated redundant mediation of the class C associated functions by OsMADS3 and OsMADS58. He also observed strong defects in stamens and carpels of osmads3 flowers, whereas most of the osmads58 flowers were indistinguishable from wild type flowers. The contribution of OsMADS3 in specifying C-function seems to be more important when compared with OsMADS58, consistent with the reports of Yamaguchi et al. [98]. The double mutants of osmads3 and osmads58 were corresponding to the ag mutant of Arabidopsis with some differences between their phenotypes. The osmads3 and osmads58 mutants showed homeotic conversion of stamens and carpels into lodicule and palea-like structures, respectively. Dreni et al. [92] also reported FM determinacy by AG subfamily genes. Out of four AG subfamily genes in rice, three (OsMADS3, OsMADS13, and OsMADS58) redundantly regulated the FM determinacy. All the three possible double mutant combinations (osmads3 and osmads58, osmads3 and osmads13, and osmads13 and osmads58) resulted in an enhanced FM indeterminacy.

Maize has three class C genes: Zea mays AGAMOUS1 (ZAG1), ZMMS2, and ZMM23 [152,153]. Like rice class C genes, ZAG1 and ZMM2 both have functional diversification as these are orthologs of OsMADS58 and OsMADS3, respectively. Expression analysis detected ZAG1 transcript abundance in early stamen and carpel primordia with partial floral meristem determinacy [97]. However, a later study with ZAG1 mutants demonstrated a loss of floral meristem determinacy with little change in stamen and carpel identity [96]. ZMM2 transcripts were expressed in stamens and carpels, while stronger expression patterns were detected in stamens only, suggesting an involvement in stamen and carpel development. Although, ZMM2 mutants have not been identified, these observations indicate overlapping but nonidentical activities for both maize C class genes.

Like rice, Brachypodium also has two C class genes—BdMADS14 and 18—that show high sequence similarity with OsMADS3 and OsMADS58, respectively [31]. Strong expression of BdMADS18...
was detected in stamens and carpels, whereas BdMADS14 was weakly expressed in stamens only. In contrast to their rice homologs, where OsMADS3 and OsMADS58 have important roles in floral organ identity [98]; the gene BdMADS18 appears to have a more dominant role in stamen and carpel identity. Similarly, wheat also has two orthologs of AG; wheat AGAMOUS-1 and 2 (WAG-1 and WAG-2) [94]. However, unlike rice and maize orthologs, these have possible roles in ectopic ovule formation and the conversion of stamens into pistil-like structures. Meguro et al. [95] reported that WAG transcription levels were low in young spikes but increased during later stages of spike development and were highest between the booting and spike emergence stages. WAG was expressed in both reproductive and non-reproductive parts of the flower with an extra transcript of WAG detected in the pistillody line. These observations suggest that WAG is associated with pistillody induction. Loss-of-function analysis of WAG genes would further elucidate their role in stamen and carpel identity. Other names for WAG-1 and WAG-2 are TaAG1 and TaAG2/TaAGL39, respectively [117,131]. Phylogenetic analysis showed that rice class C genes, OsMADS58 and OsMADS3, are orthologous to WAG-1 and WAG-2, respectively (Figure 3). In conclusion, both class B and C genes in wheat appear to have a role in the induction of pistillody [77,79,95].

Previous studies demonstrated that class D is a more specialized version of class C and define ovule identity [37,153]. Class D genes were first identified in Petunia as FLORAL BINDING PROTEIN 7 and 11 (FBP7, FBP11). Their cosuppression transforms ovules into carpelloid structures [157]. Overexpression of FBP11 results in ectopic ovules on sepals and petals [33] indicating its function in ovule identity. In Arabidopsis, class D gene functions are specified by SEEDSTICK (STK). Biochemically, STK protein interacts with class C (AG, SHP1 and SHP2) and class E proteins to define ovule identity [101]. Triple mutants of STK, SHP1, and SHP2 transform ovules into carpelloid structures [57] confirming that Class D genes specify ovule identity in Arabidopsis. Phylogenetic analysis clustered STK and SHPs into single clade (Figure 3). The functional divergence between STK and SHP paralogous genes may arise due to diversification in their DNA binding site motifs or through alterations in their tissue-specific expression levels [158]. Rice contains two orthologs of STK: OsMADS13 and OsMADS21 [99]. Expression analysis, loss-of-function and protein–protein interaction studies suggest that OsMADS13 is involved in ovule identity [99,100,102,103]. Moreover, OsMADS13 acts synergistically with OsMADS3 (a class C gene) to regulate ovule development and floral meristem termination [159]. Loss-of-function in OsMADS21 showed no ovule defects suggesting a loss of ovule specification by this gene [92,99].

Maize has three class D genes: ZMM1, ZAG2, and ZMM25 [62]. Phylogenetic analysis showed ZMM1 and ZAG2 to be closely related to rice OsMADS13, whereas ZMM25 had a close relationship with rice OsMADS21 [131]. Similar to Arabidopsis STK, the expression of ZAG2 was primarily identified in carpels and ovules [97,160] indicating a possible role in ovule specification.

Like rice, Brachypodium also has two D class genes—BdMADS2 and 4—orthologous to OsMADS13 and OsMADS21, respectively. Quantitative RT-PCR revealed comparable expressions of both genes in all floral organs, with the exception of carpels and ovules, where the expression of BdMADS2 was more than 5 times to that of BdMADS4 [30]. Ectopic expression of both genes in Arabidopsis demonstrated that overexpression of BdMADS4 produced more significant phenotypic changes than transgenic Arabidopsis carrying BdMADS2. Interestingly, in contrast to Arabidopsis and rice D class genes, overexpression of Brachypodium D-lineage genes did not directly affect carpel and ovule development in transgenic Arabidopsis. Further studies involving loss-of-function mutants would be required to confirm their role in ovule identity.

Wheat SEEDSTICK (WSTK) is an ortholog of Arabidopsis STK and rice OsMADS13. In wheat, its homologous genes are identified as TaAGL9 and TaAGL31 [117]. WSTK expression was observed in young to mature spikes, although its transcription was only restricted to pistils. During ovule development, the highest expression of WSTK was observed in the developing ovule of the pistils, suggesting an involvement in ovule specification and development [96]. Moreover, WSTK was expressed not only in true pistils but also in pistil-like stamens of an alloplasmic wheat line having
the *Aegilops crassa* Boiss. cytoplasm, which arose due to the homeotic transformation of stamens into pistil-like structures. During the homeotic transformation of stamens into pistil-like structures in an alloplasmic wheat line no significant difference were recorded in the expression of wheat class C gene homologs *WAG-1* and *WAG-2* [161]. Furthermore, yeast two-hybrid analysis demonstrated that the WSTK protein formed a complex with a class E protein (WSEP) [90]. These observations suggest that similar to Arabidopsis STK, wheat STK protein interacts with the E class protein to specify ovule identity providing an evidence functional conservation of class D genes in Arabidopsis and wheat.

3.4. Class E Homeotic Genes

Class E genes work in all floral organs and act as cofactors for A, B, C, and D class proteins to form higher order MADS-box protein complexes, which regulate the floral organ identity (floral quartet model) [162]. In Arabidopsis, four *SEPALLATA* genes (*SEPI-4*) have been reported and these specify sepal, petal, stamen, carpel, and ovule identity [34,35]. Knockdown of all of these genes results in the transformation of floral organs into bract-like structures and sepals.

In grasses, SEP-like genes are further classified into *SEP* and *LOFSEP* clades and AGL6-like genes [114,115,163]. The *SEP* clade in rice include OsMADS7 and OsMADS8. Cosuppression of both genes results in severe homeotic and meristematic changes in all floral organs, especially in lodicules [104]. OsMADS1/LEAFY HULL STERILE1 (LHS1), OsMADS5, and OsMADS34/PANICLE PHYTOMER 2 (PAP2) are placed into the *LOFSEP* clade [110]. Mutations in OsMADS1 produced an abnormal phenotype, which is described by the presence of lemma/palea-like leaves and lodicules [59]. Loss of OsMADS1 transforms the lemma into glume-like structures [164]. Simultaneous knockdown of OsMADS1, OsMADS5, OsMADS7, and OsMADS8 transforms the inner floral whorls into bract-like structures with no effect on the lemma [104] suggesting that OsMADS1 is associated with lemma and palea differentiation. A more recent study confirms that OsMADS1 is involved in floral meristem identity and activity because defective floral organs were observed in the outer two whorls of osmads−1 flowers [165]. Yeast two-hybrid analysis showed OsMADS1 protein to form heterodimers with B, C and, D class proteins that modulate floral meristem determinacy and organ identity. OsMADS1 and OsMADS13 regulate meristem determinacy in partially independent pathways while OsMADS17 is a direct target of OsMADS1 during floral development. OsMADS1 interacts physically and genetically with OsMADS3 and OsMADS58 to specify stamen identity and suppression of spikelet meristem reversion [165]. These findings suggest that OsMADS1, through physical and genetic interaction with floral homeotic regulators, has diversified functions in floral meristem maintenance and specification of organ identity. In contrast, mutations in OsMADS34 disturb inflorescence morphology and interfere with primary and secondary branches [111]. OsMADS34 has been shown to interact with rice class (A)-genes to define inflorescence meristem identity [112]. These observations demonstrate that *OsMADS34* plays an important role in inflorescence and spikelet meristem determination. Ren et al. [166] recently demonstrated that a new mutant allele (m34−2) of *OsMADS34* homeoetically converted empty glumes into lemma-like organs, suggesting that *OsMADS34* is required for glume specification.

The rice AGL6 clade contains two genes: OsMADS6/MOSAIC FLORAL ORGANS 1 (*MFO1*) and OsMADS17 [114,115]. Both genes specify floral organ identity, although the predominant role is played by *MFO1*. Mutant analysis showed that *MFO1* determines floral organs by synergistically interacting with all classes of homeotic genes, except class-(A) [113]. Interestingly, a null allele of *MFO1* converts all floral organs into lemma like structures, except the lemma, suggesting a critical role for *MFO1* in floral organ specification [167].

At least ten putative E class genes have been identified in maize, which can be further subcategorized into *SEP*, *LOFSEP*, and *AGL6* clades [105,109]. The *SEP* clade contains three genes (ZMM6, 7, and 27). The *LOFSEP* clade contains five genes (ZMM3, 8, 14, 24, and 31) and the *AGL6* clade contains two genes (ZAG3 and 5). Sequence and phylogenetic analysis showed that ZMM3 was orthologous to OsMADS5, ZMM6 was orthologous to OsMADS7, ZMM7 and ZMM27 were orthologous...
to OsMADS8, ZMM24 and ZMM31 were orthologous to PAP2/OsMADS34, and ZMM8 and ZMM14 were orthologous to LHS1/OsMADS1 (Figure 3). During spikelet development, ZMM8 and ZMM14 were expressed in upper florets, although not in the lower florets of floral organs [109], indicating a possible role in floral meristem determinacy. In situ hybridization showed that ZMM6 and ZMM27 were strongly expressed during the maize kernel development, with lower expression during inflorescence development and no expression at all during vegetative growth [105]. Furthermore, neither single nor double knockdown mutants of ZMM6 and/or ZMM27 resulted in kernel abnormalities or alterations in flower development indicating functional redundancy of class E genes in maize.

Similar to rice and maize, Brachypodium also contains six class-E genes—BdMADS1, 7, 11, 26, 28, and 32—which are further classified into SEp, LOFSEP, and AGL6 clades [31]. The SEp clade contains two genes—BdMADS26 and 32—both of which expressed highly in all floral organs except for the lemma and palea. The LOFSEP clade contains BdMADS1, 7, and 11. Strong expression of BdMADS7 and BdMADS11 was detected in all floral organs. On the other hand, the AGL6 clade contains only one gene—BdMADS28—which was weakly expressed in lodicules and stamens only [31]. These diversified expression patterns are consistent with those of rice and maize homologs and indicate functional divergence among different class E clades. To date, none of the SEp encoding genes has yet been functionally characterized in Brachypodium.

Wheat E class genes are also subcategorized into SEp, LOFSEP, and AGL6 clades. The SEp clade contains wheat SEp (WSEP), TaMADS1, TaAGL16, TaAGL28, and TaAGL30 genes [107,117]. In situ expression analysis showed WSEP in lodicules, stamens, and carpels during floral organ differentiation. Stronger expression of WSEP was observed in the palea after determination of floral organ identity, supporting the concept that in addition to organ differentiation, WSEP has a role in subsequent development [107]. Rice AGL6 clade gene OsMADS6 also showed palea specific expression [116]. Similar to Arabidopsis SEp3, WSEP also interacts with class B and C homeotic genes, suggesting a conserved role for grass E genes. TaMADS1 is another SEp encoding gene that is characterized as an E class gene [108] and orthologous to the rice class E gene OsMADS8/24. TaMADS1 is functionally similar to WSEP in that overexpression of both genes in transgenic Arabidopsis caused early flowering and terminal flower formation [107].

The LOFSEP clade in wheat contains eight genes: WLHS1, TaAGL3, 5, 8, 24, 27, 34, and 40. LEAFY HULL STERILE 1 (WLHS1) is an ortholog of OsMADS1/LHS1 [107,117]. High transcript levels of WLHS1 accumulate in glumes, lemma, palea, and lodicules while stamens and pistils exhibiting low levels. This differential expression behavior of LHS1 was also reported in other grass species including Avena sativa, Chasmanthium latifolium, Pennisetum glaucum, and Sorghum bicolor [168], which may be due to differences in corresponding inflorescence structures. The wheat AGL6 clade contains two genes: TaAGL6 and TaMADS37 [117]. Mutants of the wheat LOFSEP and AGL6 clades have not been identified and thus their function is unknown.

4. Non MADS-Box Genes Involved In Floral Organ Identity

Some non-MADS-box genes are also reported to regulate floral development. Mutants of rice aberrant panicle organization1 (apo1) showed phenotypic resemblance with class C gene mutants. APO1 mutants convert stamens into lodicules with extra carpels, suggesting that APO1 positively regulates class C gene functions [121,122]. Moreover, expression of the rice class C gene (OsMADS3) was reduced in apo1 mutants indicating that APO1 positively regulates OsMADS3 expression [169]. The Arabidopsis genes UNUSUAL FLORAL ORGANS (UFO) and APO1 are orthologs and both encode F-box proteins. UFO activates class B genes [123], suggesting a distinct role for both genes irrespective of their similar biochemical functions. Arabidopsis FLORICAULA (FLO)/LEAFY (LFY) and its rice ortholog RICE FLORICAULA/LEAFY (RFL)/APO2 displayed different yet overlapping functions. For example, RFL/APO2 specifies inflorescence meristem identity through interaction with APO1 [170], whereas FLO/LFY specifies floral meristem identity and activates class A, B, and C genes [171].
As described above, carpel identity is defined by class C MADS-box genes, however YABBY TFs are also reported to play a major role in carpel identity. The rice mutant _drooping leaf_ (dl) has some functional similarity to class C MADS TFs in specifying the carpel identity and mutation in _DL_ converts carpels into stamens [80]. These findings support the notion that candidate carpel identity genes in rice (class C and _DL_) redundantly regulate class C gene functions. _DL_ and the class B gene OsMADS16/SPW1 antagonize each other and this antagonism is critical to setting boundaries between stamen and carpel identity [80]. The Arabidopsis gene _CRABSCLAW_ (CRC) and rice _DL_ both encode YABBY TFs, although in addition to its function in carpel identity; CRC also has a role in nectary development [118]. The expression pattern of CRC in homeotic mutants suggests negative regulation by class-(A) and B genes. The wheat _DL_ ortholog (TaDL), which was identified by homology screening [119] and expression in alloplasmic wheat, was found in true pistils as well as pistil-like stamens, suggesting its role in carpel specification. Moreover, class B genes were not expressed in pistil like stamens indicating that _TaDL_ and class B genes are mutually antagonistic [77]. Like rice and wheat, the maize _DL_ mutants (drl1 and drl2) have been characterized and cloned. The _drl_ mutants displayed ectopic inner-whorl organs in pistillate and staminate florets [120]. Although meristem activity was influenced by the expression of the _Drl_ loci, _Drl_ transcripts were absent in floral meristems suggesting that _Drl_ genes may function autonomously. Sang et al. [125] characterised CHIMERIC FLORAL ORGANS 1 (CFO1), a MADS-box gene, which regulates floral organ identity in rice. Mutants of _CFO1_ showed disrupted marginal palea with ectopic but chimeric floral organs. Expression pattern analysis revealed that rice _DL_ was ectopically expressed in defective floral organs of _cfo1_ flowers, suggesting negative regulation between _CFO1_ and _DL_ [125].

More recently, Liu et al. [124] reported that LONG STERILE LEMMA1 (G1)/ELONGATED EMPTY GLUMES (ELE) and OsMADS34/PAP2 were associated with rice lemma development and determination of empty glume identity. Mutants of _G1/ELE_ showed homeotic transformation of empty glumes into lemma like organs. Single and double mutants of _G1/ELE_ and OsMADS1/OsLHS1 showed redundant roles for both genes in controlling empty glume identity and lemma development. Expression analysis of _G1/ELE_ in _osmads-1_ flowers and _OsMADS1/LHS1_ in _g-1_ flowers indicated that both genes are regulated through independent pathways and do not interact at the transcription level. In _G1/ELE_ mutant plants, downregulation of empty glume identity genes and ectopic expression of lemma identity genes provides strong evidence that empty glumes are in-fact sterile lemmas. Moreover, Yang et al. [126] identified a single recessive gene _lemma-distortion1_ (ld1) associated with lemma development in rice. This gene encodes a zinc finger protein. Overall these reports suggest that a plethora of non-MADS-box genes are also involved in floral organ identity in eudicots and cereals.

5. Functional Conservation and Diversification between Distinct Floral Specification Systems

If it is assumed that all angiosperms have homologous reproductive organs, then divergent angiosperm groups may have a single ancestral flower specifying genetic mechanism. The modified floral organ identity model (ABCDE) in Arabidopsis suggests occurrence of genetic interactions among floral homeotic genes. The same model can be used to interpret molecular control of inflorescence identity in other crop plants including cereals [37]. High-throughput forward and reverse genetic approaches have led to the identification, cloning, and functional characterization of several genes involved in the regulation of floral development especially in grasses. Interestingly, most of these genes exhibit highest sequence similarities and share expression patterns and functional properties with those of eudicot A, B, C, D, and E floral homeotic genes. However, some grass-specific floral regulators have also been identified that do not have eudicot homologs and perform distinct functions in grass floral development. This review integrates current knowledge of floral organ identity genes in an attempt to adopt the eudicot floral organ identity model to other crop species. Considering grass organ-identity models illustrated in Figure 2, it is apparent that further research is needed to functionally characterize maize, Brachypodium, and wheat MADS-box genes to manipulate for crop grain yield improvement.
Prior to the discovery of loss-of-function mutants, gene function was usually examined through sequence conservation and expression pattern comparisons with already characterised genes. Due to genome complexities and difficulties in the use of modern genetic approaches in grasses, very little was known about the role of MADS-box genes in controlling spikelet and floret development. However, recent studies have provided new insights into the conservation of class (A)-gene function among eudicots and cereals [65]. The mutational analyses of AP1/FUL-like genes in rice and demonstrated that in addition to their role in floral meristem identity, they also influenced the specification of palea and lodicule identities. As these grass-specific organs are thought to be homologous to eudicot’s sepals and petals, these divergent groups may share a conserved nonreproductive floral organ specification system.

Comparison of all the proposed models indicates a partially conservative, partially-diverse floral regulation among grasses and higher eudicots. Based on studies in model eudicots, gene expression patterns and mutant phenotypes appear to be consistent with functional predictions. This is essentially true for class B, C, and D MADS-box genes. Like eudicots, the functions of class B and C genes have diverged in grasses due to duplication and subfunctionalization of separate genes. For example, rice PI-like class B genes show unequal redundancy in their function. Individual mutant analysis of OsMADS2 indicates the homeotic conversion of lodicules without affecting stamens, whereas OsMADS4 shows no alteration in lodicules and stamens. Additionally, double mutants of both genes show the conversion of lodicule and stamen into palea and carpel-like structures, suggesting an equal role of both genes in stamen identity. However, OsMADS2 is more important than OsMADS4 in lodicule identity. Mutant analysis of maize PI orthologs also indicated that ZMM16/sts1 can compensate zmm16/sts1 reduction while specifying class B gene functions. However, ZMM18/sts1 cannot compensate for zmm16/sts1 reduction. Similar roles may be speculated for Brachypodium and wheat PI orthologs as BdMADS16 and WPII show sequence similarity with OsMADS4 and ZMM18, respectively, while BdMADS20 and WPI2 have greater similarity with respect to OsMADS2 and ZMM16 (Figure 3).

Subfunctionalization of duplicated genes was also observed among grass related class C genes. According to Yamaguchi et al. [98], OsMADS58 plays a major role in floral meristem determinacy with minor effects on floral organ identity; whereas OsMADS3 has a dominant role in stamen identity with a minor role in meristem determinacy. Similar findings were reported by Dreni et al. [92], in which OsMADS3 showed to regulate stamen identity compared with OsMADS58. Severe defects were observed in osmads3 mutant flowers, whereas most of the osmads58 mutant flowers were indistinguishable from the wild type flowers. Likewise, the maize orthologs ZAG1 and ZMM2 exhibit functional diversification and are homologs to OsMADS58 and OsMADS3, respectively. ZAG1 mutant showed loss of floral meristem determinacy and have a minor role in stamen and carpel identity. By contrast, ZMM2 has yet to be characterized for floral organ identity. In Brachypodium, BdMADS14 and BdMADS18 also indicated overlapping but diverse expression patterns as BdMADS14 highly expressed in stamens only compared to BdMADS18 that strongly expressed both in stamens and carpels. Based on orthologous relationships, Brachypodium and maize class C genes have overlapping but nonidentical functions, similar to rice genes. In contrast, the wheat class C genes WAG-1 and WAG-2 are involved in ectopic ovule formation and homeotic conversion of stamens into pistil-like structures and are orthologous to OsMADS58 and OsMADS3, respectively. Knockdown mutants of WAG genes will help elucidate their function in floral organ identity. Mutations in rice and maize class C genes result in homeotic conversion of stamens and carpels into lodicules and paleae-like organs, respectively. Similarly, class C gene mutations in Arabidopsis caused homeotic conversion of both reproductive organs, with few exceptions. Mutations of these genes in wheat result in ectopic ovule formation and homeotic conversion of stamens into pistil-like structures. Thus, diverse carpel specification systems operate in these two divergent groups.

Genetic interactions between rice class C and D MADS-box and non-MADS-box (DL) genes provided new insights into the partially conservative and partially diversified mechanisms regulating floral development in eudicots and grasses. Li et al. [159] studied double mutants of OsMADS3, OsMADS13, and DROOPING LEAF (DL) to investigate their role in floral development. Termination
of floral meristem determinacy and several carpelloid structures were observed in osmads3/osmads13 double mutants, while notably their single mutants lacked these alterations at all. Furthermore, gene expression and protein–protein interaction analyses revealed that both C and D class genes neither regulate nor interact at the transcription or protein levels, suggesting that class E genes would mediate their interaction to synergistically control the termination of floral meristem and ovule identity. These observations support the notion that grasses have retained their class C and D gene functions, despite undergone duplication and subfunctionalization. Dramatically, double mutants of osmads3/dl showed no AG activity, with production of lodicule-like structures within the fourth whorl and the termination of floral meristem determinacy. Mutual suppression was also absent and normal expression patterns were observed for OsMADS3 and DL genes in ectopic stamens of dl flowers and osmads3 mutants, respectively, suggesting a redundant role for both genes in floral meristem termination. In contrast, single and double mutants of OsMADS13 and DL suggest that DL is epistatic to OsMADS3, and both have identical roles in ovule identity. More recently, the role of ovule in cereal grain development has been reviewed. The phenotype of single dl mutants was identical to that of double osmads13/dl mutants. The dl mutants lacked OsMADS13 expression, whereas single mutant of osmads13 showed abundance of DL transcripts, indicating direct or indirect OsMADS13 regulation by DL. Dreni et al. investigated genetic interactions between rice class C and D genes (OsMADS13 and OsMADS58) through single- and multiple-gene mutants. As expected, osmads13/58 double mutants showed accumulation of lodicule and palea-like organs in the third and fourth whorls accompanied by loss of floral organ identity and the triggering of floral meristem indeterminacy due to reduced AG activity. These observations suggest that a highly conserved class C gene functional mechanism exists in grasses despite partial subfunctionalization among duplicated genes. These results led to the proposition that DL lacks class C gene functional activity and cannot specify carpel identity alone, requiring both OsMADS3 and OsMADS58. Although these findings provide new insights into the floral development process, further examination of single and multiple mutants of class B, C, D, and DL genes will be required to elucidate the roles of MADS-box and DL genes in floral organ specification.

The function of class E genes, particularly the SEP-like, are somewhat conserved among eudicots and grasses. In rice, detailed spatial and temporal mRNA expression studies, protein interaction patterns, and mutant analysis indicated a consistent role for SEP-like genes in floral meristem and organ identity specification, since divergence from eudicots. Mutant phenotypes of Arabidopsis SEP redundant genes (SEP1/2/3/4) and rice OsMADS1, OsMADS7, and OsMADS8 genes indicated a redundant but interdependent role for both groups, suggesting a partial overlap but subfunctionalization among class E genes. Furthermore, characterization of AGL6 clade mutants of rice and maize indicated a similar functional role in floral meristem determinacy and organ identity. Similar expression patterns of monocot AGL6 and SEP clade genes and their complex interactions with class B, C, and D genes indicated conserved floral specification systems. The functional similarity of SEP and AGL6 clades is provided by Petunia floral development genes.

6. Future Perspectives

Understanding of grass inflorescence morphogenesis has expanded significantly over the last two decades. Extensive studies in model plants have demonstrated common genetic factors regulating eudicot and grass floral development including MADS-box and non-MADS-box genes and epigenetic regulators. For Arabidopsis and rice, the genetic and molecular mechanisms of transition from vegetative to reproductive phase and the role of MADS-box genes in floral organ identity are well understood. However, this is less well defined for Brachypodium, maize, and wheat because loss-of-function mutant analysis is rare in these species. Currently, advances in genetics analysis has made mutant development and characterization easy in grasses which is being used to define grass floral developmental biology. Deciphering the molecular control of transition from shoot apical meristem to floral meristem development and the determination of floral organ identity will provide...
new insights to devise innovative strategies for the development of cereals with enhanced grain yield and adaptation to multiple environments [174].

Biological research in general and plant evolutionary biology have been revolutionized by advances in next generation sequencing. Enormous amounts of genomic and transcriptomic sequence data have also been generated through the 1000 Plants Project (1KP) and the Floral Genome Project [175,176]. These gene resources provide an unprecedented opportunity to bridge the evolutionary gap between floral morphogenesis in model plants and economically important cereals by characterizing floral genetic components of ABCD model. Here, it is important to note that most of the cereal orthologs are merely retrieved by phylogenetic analysis from resource genome databases; therefore, specified experimental studies will be required to support genetic framework of underlying mechanisms of floral organ identity in cereals. In this perspective, genome editing tools such as virus-induced gene silencing (VIGS) and clustered regularly interspaced short palindromic repeats (CRISPR)/Cas9 system has been widely useful in several eudicots and monocot species to investigate gene function in floral organ identity and symmetry between basal and core eudicots [177–181]. Effective application of these systems could herald a new generation of multidisciplinary evo–devo research that better describes the evolutionary changes in gene regulatory networks underlying floral development. Moreover, these approaches along with TILLING resources can provide new avenues for grain yield improvement in cereals through translational research.

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**Abbreviations**

| Abbreviation | Description |
|--------------|-------------|
| ABS | ARABIDOPSIS BSISTER |
| AG | AGAMOUS |
| AGL6 | AGAMOUS-LIKE 6 |
| AP1 | APETALA1 |
| AP2 | APETALA2 |
| AP3 | APETALA3 |
| APO1 | Aberrant panicle organization-1 |
| BD1 | BRANCHED SILKLESS1 |
| BdMADS | Brachypodium MADS |
| BM | Branch meristem |
| BR | Branch |
| CA | Carpel |
| CAL | CAULIFLOWER |
| CFO1 | CHIMERIC FLORAL ORGANS 1 |
| CRC | CRABSCLAW |
| DL | Drooping leaf |
| ELE | ELONGATED EMPTY GLUME |
| FBP11 | FLORAL BINDINGPROTEIN 11 |
| FBP7 | FLORAL BINDINGPROTEIN 7 |
STK  SEEDSTICK
STS1  Sterile Tassel Silky Ear1
TaAG3  Triticum aestivum AGAMOUS3
TaAP3  Triticum aestivum AP3
TaDL  Triticum aestivum Drooping Leaf
TaMADS  Triticum aestivum MADS
TFs  Transcription factors
TS  Terminal spikelet
TSM  Terminal spikelet meristem
TT16  TRANSPARENT TESTA 16
UFO  UNUSUAL FLORAL ORGANS
VRN1  VERNALIZATION 1
WAG-1  Wheat AGAMOUS-1
WAG-2  Wheat AGAMOUS-2
WAP1  Wheat APETALA1
WAP3  Wheat APETALA3
WBsis  Wheat BSISTER
WFUL1  Wheat FRUITFULL 1
WFUL2  Wheat FRUITFULL 2
WFUL3  Wheat FRUITFULL 3
WLHS1  Wheat LEAFY HULL STERILE 1
WPI1  Wheat PISTILLATA 1
WPI2  Wheat PISTILLATA 2
WSEP  Wheat SEPALLATA
WSTK  Wheat SEEDSTICK
ZAG1  Zea mays AGAMOUS1
ZAG2  Zea mays AGAMOUS2
ZAP1  Zea mays APETALA1
ZmlIDS1  Zea mays INDETERMINATE SPIKELET1
ZMM  Zea mays MADS

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