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Review

Variations on a theme: Changes in the floral ABCs in angiosperms

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ABSTRACT

Angiosperms display a huge variety of floral forms. The development of the ABC-model for floral organ identity, almost 20 years ago, has created an excellent basis for comparative floral development (evo-devo) studies. These have resulted in an increasingly more detailed understanding of the molecular control circuitry of flower development, and the variations in this circuitry between species with different types of flowers. In this review, we analyze the variations in the molecular control of floral organ development: the changes in the floral ABCs. In addition, we discuss the control and diversification of inflorescence architecture, as this is another important source of structural diversity between flowering species.

Contents

1. Introduction

One of the most important contributions to our understanding of flower development was the formulation of the classic ABC-model for floral organ identity, by now almost 20 years ago. This model was based on an interpretation of Arabidopsis and Antirrhinum mutants [1], although in the first version of the Antirrhinum model no A-function was included [2]. In the early nineties, genes encoding B- and C-functions were cloned from both species, all of them members of the MADS-box gene transcription factor family [3–8]. A-function representatives were only cloned from Arabidopsis, and appeared to be an *AP2* transcription factor gene [9] and the MADS-box gene *AP1* [10].

The striking overall similarities in B- and C-function regulation between Arabidopsis and Antirrhinum, while fairly distantly related within the core eudicots, led to the assumption of a universal applicability of the ABC-model, although this viewpoint was not necessarily shared by the original authors and other researchers. Nevertheless, the development of the ABC-model was a major breakthrough in the understanding of floral development and has acted as a catalyst for comparative floral development studies (floral evo-devo). These have resulted in a presently much better understanding of the variation in the molecular control of the development of different types of flowers.

In general, we can distinguish two types of variability:

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(1) Variations in the molecular networks controlling flower development, between species with similar flower architecture. A large proportion of this variability can be explained by lineage-specific differences in gene duplications and the subsequent functional diversification, leading to variations in functional redundancy, gene loss, and subfunctionalization. Moreover, there are indications that some aspects of the regulatory network are not conserved between certain species, although the final result, a four-whorled flower with sepals, petals, stamens and carpels, is the same. This demonstrates the plasticity of (molecular) evolution to generate different mechanisms to control the same process.
(2) Variations between species with flowers with different architectures. Given the enormous variation in floral forms among angiosperms, it is obvious that important ABC regulatory changes can be expected in flower types that deviate from the general sepal–petal–stamen–carpel set-up. Classic examples can be found in the monocots, such as the tulip flower, and the flowers of grasses which develop palea/lemma and lodicules rather than sepals and petals.

This chapter is complemented with a section on diversity of inflorescence architecture, which forms another important source of variation between flowering species.

2. Variations in the control of floral organ development

2.1. The A-function

In Arabidopsis the A-function has been attributed to two genes: MADS-box gene *APETALA1* (*AP1*) and *AP2*/*ERF* transcription factor *APETALA2* (*AP2*) [9,10]. In mutants of these genes, the sepals are transformed into leaf- or bract-like organs (or develop carpelloid features), and the petals are either absent or transformed into stamen-like structures. These genes thus appear to be required for the correct specification of the identity of sepals and petals. It is debatable whether *AP1* and *AP2* truly function as perianth organ identity genes (reviewed in [11]), they more likely "specify" organ identity indirectly by establishing the floral meristem [12] and by restricting C-function gene expression to the inner floral whorls [13,14]. Functional studies on *AP1* lineage genes from other species indicate that the role of *AP1* in floral meristem specification is most likely conserved in other eudicot species, while the contribution of the gene to perianth formation is not (reviewed in [11]).

In Arabidopsis, the crucial role of the *AP2* gene in suppressing *AGAMOUS* (*AG*) in the perianth, in turn is regulated by the microRNA *AtmiR172* [15]. Recently, doubt has arisen about the universality of the role of *AP2* genes in C-function gene regulation (e.g. [11]). Mutants of Petunia and Antirrhinum *AP2* orthologs did not exhibit the same phenotype as Arabidopsis *ap2* mutants [16,17]. The *blind* (*bl*) mutant in Petunia and *fistulata* (*fis*) mutant in Antirrhinum, however, display a partial A-function phenotype, producing flowers with petals converted to antheroids [18–20].

Cartolano et al. [21] demonstrated that *BL* and *FIS* encode a homologous microRNA from the *miR169*-family. *BL* (Petunia) and *FIS* (Antirrhinum) are required to confine C-gene expression to the inner two floral whorls. Suppression is indirect, since C-function MADS-box genes do not harbor a *miR169* target site sequence and thus cannot be direct targets. *miR169* microRNAs are thought to target mRNAs of the *NF-YA* transcription factor family [22]. As NF-Y transcription factor complexes can activate target genes via CCAAT-boxes, which are present in the introns of C-function genes, Cartolano et al. [21] proposed that NF-YA members might be able to upregulate C-function gene expression. In this way, *miRBL* and *miRFIS* would repress expression of C-function genes by post-transcriptional repression of NF-YA members, although evidence for this is still lacking.

Two completely different mechanisms thus appear to have evolved to serve the same function: restricting C-function gene activity to the inner two floral whorls. This is clearly an example of variation in molecular networks without a structural difference in flower make-up. Remarkably, the elements of the miR169-*NF-YA* machinery are also present in Arabidopsis, while the *AP2*-miR172 elements can be found in Antirrhinum and Petunia. Future research will show whether these complementary mechanisms have lost some or all function, and/or acquired new ones. Moreover, it is important to examine which of the two mechanisms (or indeed yet other mechanisms) of restricting C-function gene activity to the center of the flower are employed by other angiosperm species. This information can than help us to unravel the evolutionary history, and level of conservation, of the miRNA169 and miRNA172 pathways.

2.2. The B-function

Arabidopsis and Antirrhinum both contain two B-function genes (*APETALA3*, *AP3* plus *PISTILLATA*, *PI*; and *DEFICIENS*, *DEF* plus *GLOBOSA*, *GLO*, respectively), which are required to specify petal and stamen identity in the second and third floral whorls. All of their single mutants display the same homeotic transformation of petals to sepals and stamens to carpels. This is in accordance with the activity of the encoded proteins, DEF and GLO in Antirrhinum and AP3 and PI in Arabidopsis, as obligate heterodimers [3,4]. The expression of either of the B-function genes is initiated independently in the second and third floral whorls, but the maintenance of high levels of *DEF* and *GLO* or *AP3* and *PI* by autoregulation depends upon the presence of the heterodimeric protein complex (Fig. 1) [23–26].

While the *DEF*/*AP3* and *GLO*/*PI* lineages originated from a gene duplication that happened an estimated 260–290 MYA [27,28], it has become clear that in many species the B-function has been further shaped and complicated by other rounds of gene duplications in both gene lineages. Of special interest for the evolution of the core eudicot flower, is a duplication in the *DEF*/*AP3* lineage which coincided with the radiation of the core eudicots, and resulted in the eu*AP3* lineage (to which *DEF* and *AP3* belong) and the *TM6* lineage [29]. euAP3 and TM6 proteins can easily be distinguished by their distinct C-terminal motifs, the so-called eu*AP3* and paleo*AP3* motifs. Proteins containing a paleo*AP3* motif can be found throughout the angiosperms, while eu*AP3* motif containing proteins are found only in the core eudicots. Remarkably, the eu*AP3* C-terminal motif seems to have originated from the paleo*AP3* motif by a frameshift mutation [30,31]. Many core eudicots have retained both eu*AP3* and *TM6* gene copies, while Arabidopsis and Antirrhinum both have lost the *TM6* gene [29,32]. As a consequence, the function and regulation of *TM6* genes was not included in the original ABC-model.

An early indication that B-function gene regulation might deviate from the original ABC-model in some eudicot species, despite having a similar floral architecture as Arabidopsis and Antirrhinum, came from a homeotic Petunia mutant, called *green petals* (*gp*, now *Petunia hybrida DEFICIENS*, *PhDEF*) [33]. In this null mutant, petals fully convert to sepals, but stamen development is unaffected. The reason behind this aberrant phenotype was only discovered by a functional analysis of the Petunia B-function genes that also included the *TM6* gene copy (*Petunia hybrida TM6*, *PhTM6*) [32,34]. While all aspects of B-regulation described for Arabidopsis and Antirrhinum appear to be conserved for the duplicated pair of Petunia *PhGLO* genes and for *PhDEF* (*GP*), *PhTM6* clearly does not obey the ABC rules (Fig. 1). *PhTM6* is most highly expressed in whorls three and four, it does not require functional *GLO* proteins

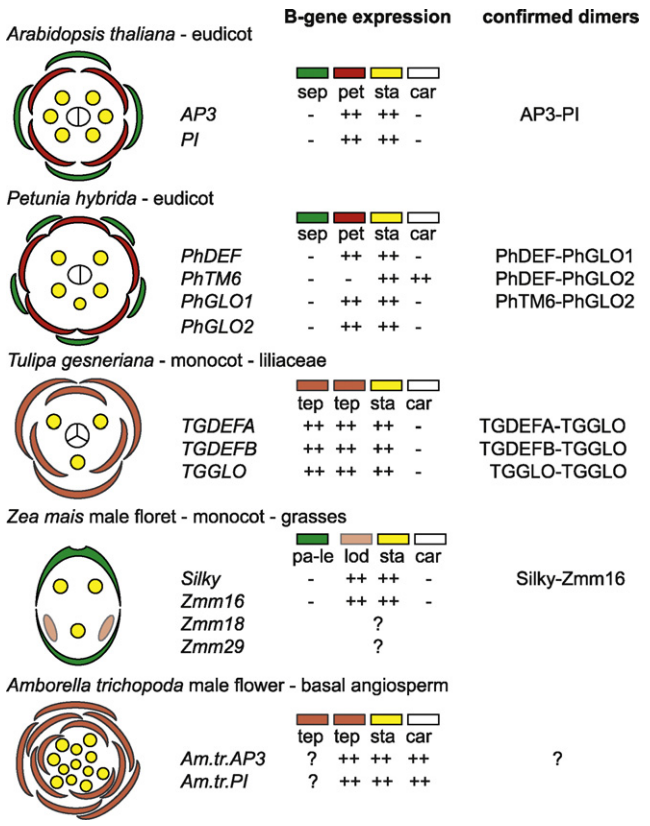

Fig. 1. B-gene function in a selection of angiosperm species. Flower diagram (left), B-gene expression (middle) and confirmed B-protein dimers (right) for *Arabidopsis thaliana* [4], *Petunia hybrida* [34], *Tulipa gesneriana* [39], *Zea mais* [47], and *Amborella trichopoda* [42]. (++) Indicates high levels of gene expression and (–) indicates a relatively low level or no expression. *Abbreviations*: sep, sepal; pet, petal; sta, stamen; car, carpel; tep, tepal; pa-le, palea and lemma; lod, lodicule.

to maintain high expression levels, and is not involved in petal identity control. Rather *PhTM6* specifies stamen identity in a fully redundant fashion with *PhDEF* [32]. In fact, all *TM6* genes analyzed so far, including representatives from Petunia, tomato, grape and Gerbera, tend to be expressed at lower levels in the petals, while they are expressed at high levels in stamens and carpels [32,35–37].

The clear difference in function between eu*AP3* and *TM6* genes, at least in Petunia, seems to be largely attributable to a different regulation of the two proteins: a highly conserved and functionally essential 5′ regulatory element present in eu*AP3* type promoters [38] is completely absent in the *PhTM6* 5′ regulatory unit. Although *PhTM6* is not involved in petal identity control, it can rescue petal development in a *phdef* mutant background when expressed from a constitutive promoter [32]. It therefore seems that the differences in protein sequence between *TM6* and eu*AP3* genes have not had a major impact on their functional diversification.

Other examples of a different set-up of B-class regulation or -function can be found in the monocots, in which two main floral forms can be distinguished.

Animal attracting monocots (e.g. tulips and lilies) have petaloid organs, called tepals, in both the first and second whorls, which have been associated with expansion of the B-gene expression domain to the first floral whorl (Fig. 1) (e.g. [39]). This observation gave rise to the "sliding boundary" hypothesis, which describes how floral diversity can be achieved by outward or inward shifts of B-function gene expression ([40], reviewed in [41]). An analogous "fading borders" model has been proposed to explain gradual transitions in organ morphology in some basal angiosperms (Fig. 1) ([42,43], reviewed in [41]). However, the molecular changes that have allowed modulation of the B-function domain remain to be determined.

In grasses on the other hand, regulation and expression of B-genes in the second and third floral whorls is well conserved [44–47], but in the second floral whorl, where in eudicot flowers petals form, most grasses produce lodicules: small scale-like or fleshy organs that swell at anthesis to open the floret (Fig. 1). Since maize B-function genes are capable of rescuing the corresponding Arabidopsis B-function mutant phenotypes [47], phenomena like these are probably best explained by changes in the target genes of the B-function transcription factors. It will be interesting to try to find out what changes in target genes have occurred and whether changes in the B-function proteins themselves or their interacting partners might have played a role in this.

2.3. The C- and D-function

The Arabidopsis C-function gene *AGAMOUS* (*AG*) is involved in the specification of male and female reproductive organ development and in regulating floral meristem determinacy [7,48]. Two additional Arabidopsis *AG* subfamily genes, *SHATTERPROOF1* (*SHP1*) and *SHP2*, share largely redundant functions in specifying the fruit dehiscence zone, and function together with *AG* in carpel development [49,50]. Another closely related Arabidopsis gene is the D-function gene *SEEDSTICK* (*STK*). *STK* is involved in ovule development, and is required for dispersal of the seeds when the fruit matures [50]. In promoting ovule identity, *STK* acts redundantly with *SHP1*, *SHP2* and *AG* [50]. The D-function was originally discovered in Petunia [51] and added several years after the ABC-model was originally proposed, to represent genes involved in regulating ovule development. As D-function genes belong to the same MADS-box gene subfamily as C-function genes and several C-function genes were shown to share functions in ovule development with D-function genes, the D-function genes are perhaps better regarded as more specialized C-function genes.

A gene duplication event early in angiosperm evolution led to the divergent C- and D-function gene lineages (*AG* clade and *FLORAL BINDING PROTEIN7/11* (*FBP7/11*) clade, respectively). Representatives of the D-lineage appear widely conserved across the angiosperms [52]. Thus far, most identified *FBP7/11* clade (D-lineage) genes, including core eudicot and grass orthologs, exhibit ovule-specific expression (e.g. [50,51,53–55]). Functional studies in Petunia and rice have shown that the role of D-function genes in the regulation of ovule development is largely conserved between these two species and Arabidopsis (reviewed in [56]).

More recent gene duplications have taken place in the *AG* clade (C-lineage) both within the grasses [57,58] and the eudicots [52]. These have been followed by functional diversification of the gene copies, resulting in subfunctionalization and probably also neofunctionalization. Comparative analysis of the Arabidopsis and Antirrhinum *AG* clade genes shows the randomness of subfunctionalization: the genes that are involved in the primary aspects of C-function, *PLENA* (*PLE*) and *AG*, respectively, are actually paralogs [59]. As the divergence of functions between the different *AG* paralogs in rice and maize is so similar, it is likely that subfunctionalization of these grass *AG* clade genes has begun before the divergence of these two species [57,58]. Remarkably, in rice, C-function genes might act in conjunction with the *YABBY* gene *DROOPING LEAF* (*DL*) to specify carpel identity [60]. This mechanism seems not conserved in Arabidopsis, as the Arabidopsis *DL* ortholog, *CRABS CLAW* (*CRC*) plays only a partial role in carpel identity [61].

Even the *AG* subfamily genes of the most basal angiosperms and gymnosperms are expressed in the reproductive tissues, which sug-

gests a deeply conserved role in the production of these tissues (e.g. [42,62,63]). Overall, the C/D-function is probably the most conserved gene function among the MADS-box genes, even though many subfunctionalization events and several neofunctionalization events have taken place after gene duplications within the *AG* subfamily. It is interesting to speculate about the reason for the high level of conservation for this gene function. It has been suggested before that there might be a constraint on paralogs within a species such that the sum total of all functions must cover at least the ancestral function, especially for the *AG* subfamily, because of the critical role *AG* homologs play in reproduction [64]. To fully uncover the levels of redundancy, and events of subfunctionalization and neofunctionalization within the *AG* subfamily it will be necessary to functionally analyze the complete set of *AG* subfamily members from other species, as was done for Arabidopsis [50]. Such an extensive analysis performed on a number of phylogenetically well chosen species could also shed light on the meaning of the C/D-lineage split.

2.4. The E-function

The E-function was not included in the original ABC-model, but added later as it became clear that the A-, B-, and C-function genes need other co-factors to produce floral organs [65–68]. Floral organ identity is proposed to be regulated by multimeric complexes of ABCDE proteins (floral quartet model; [69]). In these complexes the B-, C-, and D-function proteins are thought to be important for organ-specific gene regulation, while the E-function proteins act as the mediators for the formation of the protein complexes (e.g. [70,71]).

The E-function in Arabidopsis is encoded by genes from the angiosperm-specific *SEPALLATA* (*SEP*; previously called *AGAMOUS-LIKE2*, *AGL2*) MADS-box gene subfamily [67]. Arabidopsis harbors four *SEP* subfamily genes: *SEP1–4*. The Arabidopsis *sep1 sep2 sep3* triple mutant produces sepals in all floral whorls (hence the subfamily name *SEPALLATA*) and shows loss of meristem determinacy in the center of the flower [67]. Addition of the *sep4* mutation resulted in the conversion of all floral organs into leaves [72]. Thus, only the quadruple mutant exhibits a complete loss of floral organ identity. The four Arabidopsis *SEP* genes show a high level of functional redundancy, though the different genes also demonstrate some diversification in functions (e.g. [73]).

Multiple *SEP* homologs are present in distantly related angiosperm lineages, suggesting that the *SEP* subfamily has experienced several early gene duplication events. The two major lineages, the *AGL9* and the *AGL2/3/4* clade, are most likely the result of a pre-angiosperm duplication, as representatives of both clades are present in the basal angiosperm Amborella [74]. Additional gene duplications have occurred in eudicots and the grass monocots [74].

As most species have multiple *SEP* gene copies with often redundant functions, there is only limited functional data available for *SEP* genes. So far only two out of the six Petunia *SEP* genes have been analyzed in detail. Together with a study in Arabidopsis [73], this proved that also the D-function requires SEP activity [75]. Despite a high level of functional redundancy, the Petunia *SEP* gene copies do also exhibit diversification in function. Also the two functionally analyzed Gerbera *SEP* genes show signs of subfunctionalization: *GERBERA REGULATOR OF CAPITULUM DEVELOPMENT1* (*GRCD1*) has a function, specifically in whorl three, while *GRCD2* has a function, specifically in whorl four [76,77]. The tomato *LeMADS-RIN* gene was also shown to have a unique function: the gene seems involved in the ripening of the tomato fruit [78]. The highly variable expression patterns of the grass *LHS1* lineage *SEP* genes in different species suggest variation in their function in specifying organ identity and determinacy of the spikelet meristem [79]. Functional diversification of these genes is thought to have played a role in the diversification of spikelet morphology [80].

In general, the number of *SEP* genes and their expression patterns vary between species. The contribution of specific *SEP* genes to various aspects of flower development differs. Still, all available data seem to indicate a general function of SEP proteins as mediators of the formation of a set of protein complexes. So far, it has been impossible to determine if there are conserved functions specific to *SEP* gene lineages. Only by obtaining more functional data we can figure out the exact functions of all *SEP* genes.

Interestingly, extant gymnosperms do not seem to harbor any *SEP* genes. They do however contain the closely related *AGAMOUS-LIKE6* (*AGL6*) genes (reviewed in [41,81]). Recently, Rijpkema et al. [82] showed that the *Petunia hybrida AGL6* gene (*PhAGL6*, formerly called *PETUNIA MADS BOX GENE4*, or *pMADS4*) functions redundantly with the *SEP* genes *FBP2* and *FBP5* in petal and anther development. Around the same time, the characterization of two more *AGL6* gene mutants was published: both the maize *bearded-ear* (*bde*) gene and the rice *MOSAIC FLORAL ORGANS1* (*MFO1*) gene are involved in the regulation of floral organ identity and floral meristem determinacy [83,84], and seem to function like *SEP* genes. The expression pattern of the Petunia *AGL6* gene, and that of its homologs from other species [82,85,86], further hints at a role in ovary, ovule and/or gametophyte development, possibly redundant with other (*SEP*) MADS-box genes. Conservation of a *SEP*-like function for both Petunia, maize and rice *AGL6* genes indicates that comparative *SEP* functional analyses should also include members of the *AGL6* subfamily. It will be interesting to find out to what extent *AGL6* genes from other species, especially gymnosperms, perform a similar function.

3. Control and diversification of inflorescence architecture

Angiosperms widely diverged with regard to the moment (i.e. the season and/or the plant age) that they switch to flowering as well as to the number and position of flowers that are formed. Some species generate a single (solitary) flower at the end of a shoot, while others generate clusters of flowers, known as inflorescences. Inflorescences can be divided into three major classes based on their mode of development (Fig. 2) [87–89]. In racemes the shoot apical meristem grows indefinitely (i.e. it is indeterminate). It generates lateral meristems that terminate by forming a flower, resulting in a straight axis with many lateral flowers. In cymes, the apical meristem is determinate and terminates by forming a flower while growth continues from a lateral (sympodial) meristem that forms the next “sympodial” inflorescence unit. Panicles occupy an intermediate position: both apical and lateral meristems initially continue to grow and generate more lateral meristems and at some point they all terminate by forming a flower.

Theoretical modeling indicates that inflorescences may have diverged by alterations in the spatio-temporal regulation of genes specifying floral or shoot fate of meristems [89]. In a variety of species, floral meristem identity is specified by widely conserved transcription factors known as LEAFY (LFY) and APETALA1 (AP1) in Arabidopsis, together with the F-box protein UNUSUAL FLORAL ORGANS (UFO). Mutations in *LFY* and *AP1* homologs (partially) convert flowers into inflorescence shoots in a variety of species (reviewed in [88]). The importance of *UFO* was initially underestimated as *ufo* mutations have at most a very weak floral meristem identity phenotype and primarily affect the development of petals and stamens in the flower [90,91]. In contrast, mutations in the Petunia and tomato *UFO*-orthologs *DOUBLE TOP* (*DOT*) and *ANANTHA* (*AN*) almost completely block floral identity [92–94]. The weak *ufo* phenotype seems to be due to genetic redundancy as expression of a dominant negative form of UFO in Arabidopsis results in a strong flower-to-shoot transformation [95].

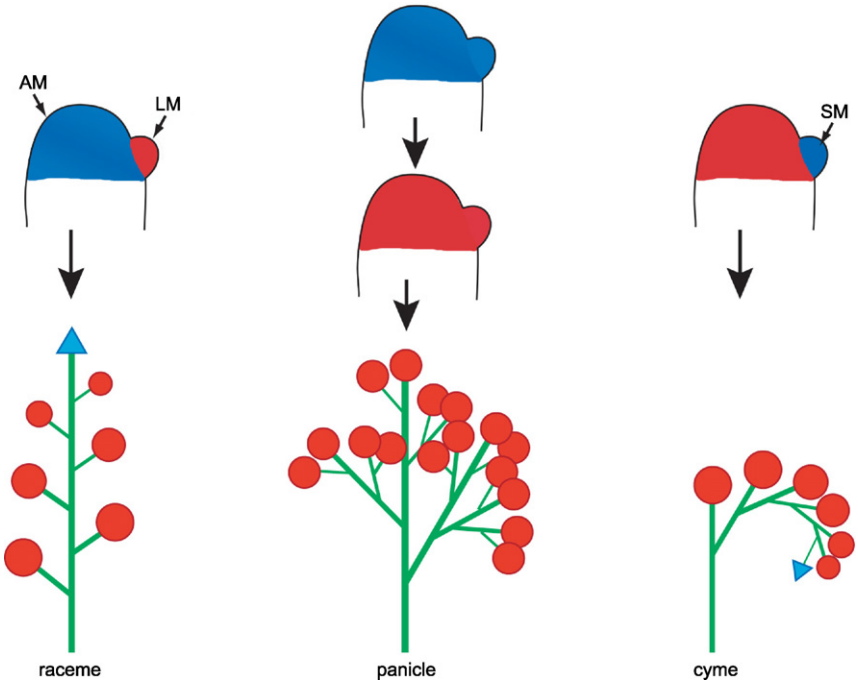

Fig. 2. Schematic representation of the development and architecture of the three major inflorescence types. Top: diagrams showing the relative position and developmental fate or identity of apical and lateral meristems in distinct inflorescences. Red color indicates floral identity, blue color non-floral or shoot identity. Bottom: diagrams of fully developed inflorescences. Flowers are indicated by red circles, meristems by blue triangles. am, apical meristem; lm, lateral meristem; sm, (lateral) sympodial meristem.

Although these floral identity genes encode very similar and functionally exchangeable proteins [92,96], their expression pattern and genetic regulation diverged widely suggesting that the upstream transcriptional circuitry has been extensively rewired during evolution [92]. For example, in Arabidopsis, UFO is expressed in the inflorescence in lateral (floral) meristems, but also on many sites that lack floral identity [97,98]. Moreover, constitutive expression of UFO or the Petunia ortholog DOT does not alter the timing and positioning of flowers [92,97]. The limiting factor that determines when and where flowers are formed in Arabidopsis is the transcription of *LFY* and its immediate target *AP1*. *LFY* expression increases during the vegetative phase and when it reaches a certain threshold flowering commences [99–101]. *LFY* and *AP1* expression in the inflorescence is restricted to the lateral floral meristems and is excluded from the apical inflorescence meristem [10,102]. If, however, *LFY* or *AP1* are constitutively expressed, precocious flowering occurs and the inflorescence apex converts into a solitary flower [103,104].

Cymes require a more complex regulation of floral fate as both apical and lateral meristems ultimately form flowers, but with a different timing [89]. In cymes like Petunia and tomato, the *LFY*-homologs *ABERRANT LEAF AND FLOWER* (*ALF*) and *FALSIFLORA* (*FA*) are expressed in a different and wider pattern than *LFY* [105,106]. *ALF* and *FA* are expressed during the vegetative phase, while in the inflorescence they are first expressed in apical meristems and with some delay in lateral meristems. The *UFO*-homologs *DOT* and *AN*, however, are expressed in a narrower pattern than *UFO*, as they are only active during flowering within apical (floral) meristems, while their expression in lateral meristems is delayed, much more than that of *ALF* [92,94]. That the transcription of *DOT* rather than *ALF* is the factor that delimits the formation of flowers in Petunia is supported by the observation that constitutive expression of *DOT* or *UFO* triggers precocious flowering, partially transforms leaves into petals and converts the cyme into a solitary flower – apparently because floral identity is no longer repressed in lateral inflorescence meristems [92].

Recently a new regulator was discovered that seems specific for cymes. *EVERGREEN* (*EVG*) from Petunia and *COMPOUND INFLORESCENCE* (*S*) of tomato encode a WUSCHEL-RELATED HOMEOBOX (WOX) transcription factor that is required for floral identity. A (near) null *evg* mutation strongly reduces *DOT* expression and converts flowers into shoots [107]. Tomato *s* mutants display a weaker phenotype, possibly because the 3 *s* alleles – two missense alleles and an unsolved rearrangement – are not null. *AN* expression in these *s* mutants is reduced rather than abolished and the formation of flowers is delayed rather than completely inhibited, resulting in increased branching and a more compound inflorescence [94]. Surprisingly, *EVG* and *S* are not expressed in the apical floral meristem where *DOT* is active, but in the newly emerging lateral sympodial meristem shortly before it becomes visible as a separate dome. This together with the finding that mutations like *extrapetals* and *hermit*, which convert the cyme into a solitary flower [105,108], fully repress the floral identity defect of *evg*, indicates that *EVG* promotes *DOT* expression and floral identity indirectly by an unknown mechanism [92].

EVG arose as a paralog of a deeply conserved *WOX* gene represented by *SISTER OF EVERGREEN* (*SOE*) in Petunia and *WOX9*/*STIMPY* and *WOX8*/*STIMPY-LIKE* in Arabidopsis [107], which are expressed throughout plant development and have important roles in patterning of the embryo and maintenance of a variety of meristems [109–111]. Since Arabidopsis lacks a true *EVG* homolog with a similar expression pattern and since *EVG* is fully redundant in Petunia mutants with solitary flowers, it presumably represents a key factor in the evolution of cymose architecture. Given that tomato *s* mutants phenocopy the more compound cymes of other Solanaceae, it appears that modulation of *EVG*/*S* activity was also important for the further diversification of cymes [94].

4. Conclusion

Evo-devo studies on floral development confirm once more the principle of 'never change a winning team' in the sense that

the team members largely remain the same. The combinatorial recruitment of MADS-box proteins to specify floral organ identity in angiosperms appears to be cast in iron. The majority of variations on the ABC theme thus far seem to reside in the regulatory circuitry of this winning team, rather than in changes in the protein structure of the respective team members. Better understanding of angiosperm floral diversity at the molecular level therefore might be obtained from an increased focus on the evolution of both cis and trans ABC regulatory elements and variations in downstream target gene control. That being said, it is astonishing to see how in different species sometimes different genes are involved in controlling the same structure (C-function control) and sometimes the same genes induce different structures (LEAFY and UFO in diverse inflorescence types).

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