Circlize package in R and Analytic Hierarchy Process (AHP): Contribution values of ABCDE and AGL6 genes in the context of floral organ development

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Abstract

The morphological diversity of floral organs can largely be attributed to functional divergence in the MADS-box gene family. Nonetheless, research based on the ABCDE model has yet to conclusively determine whether the AGAMOUS-LIKE 6 (AGL6) subgroup has a direct influence on floral organ development. In the current study, the ABCDE model was used to quantify the contributions of ABCDE and AGL6 genes in the emergence of floral organs. We determined that the flower formation contribution values of the ABCDE and AGL6 genes were as follows: A gene, 0.192; B gene, 0.231; CD gene, 0.192; E gene, 0.385; and AGL6, 0.077. As AGL6 does not directly influence floral structure formation, the contribution value of AGL6 to flower formation was low. Furthermore, the gradient values of the floral organs were as follows: sepals, 0.572; petals, 1.606; stamens, 2.409; and carpels, 2.288. We also performed detailed analysis of the ABCDE and AGL6 genes using the Circlize package in R. Our results suggest that these genes likely emerged in one of two orders: 1) B genes → CD genes → AGL6 → E genes → A genes; or 2) B genes → CD genes → AGL6/E genes → A genes. We use the analytic hierarchy process (AHP) to prove the contribution values and gradient values of floral organs. This is the first study to understand the contribution values of ABCDE and AGL6 genes using the AHP and the Circlize package in R.

Introduction

The importance of MADS-box genes in the emergence of floral structures and subsequent morphogenesis makes them an ideal tool to examine the development of floral structures [1–3]. The nomenclature of this family is based on the members that were first identified: MINI-CHROMOSOME MAINTENANCE 1 (MCM1) from Saccharomyces cerevisiae, AGAMOUS (AG) from Arabidopsis thaliana, DEFICIENS (DEF) from Antirrhinum majus, and SERUM RESPONSE FACTOR (SRF) from Homo sapiens [4,5]. It is generally presumed that an ancestor
of the MADS-box gene developed prior to the evolution of eukaryotes, after which it evolved into two main clades, type I (SRF-like) and type II (MEF2-like) [6]. Among terrestrial plants, the structure of type II MADS-box transcription factors (TFs) comprise a MADS (M)-domain followed by an intervening (I), keratin-like (K), and C-terminal (C) domain (i.e., MIKC-type) [7,8]. MIKC-type TFs are further divided into MIKC$^{-}$- and MIKC$^{C}$-type [9].

The ABCDE model posits that among MIKC$^{C}$-type TFs, members of the ABCDE and AGAMOUS-LIKE 6 (AGL6) subgroups play a key role in the development of floral organs (Fig 1) [3,5,10]. The ABCDE and AGL6 genes form five subgroup clusters, namely APETALA1 (AP1 or A), AP3/PISTILLATA (AP3/PI or B), AG/SHATTERPROOF/SEEDSTICK (AG/SHP/STK or CD), SEPALLATA (SEP or E), and AGL6/AGL13 (AGL 6). Essentially, A, B, and C proteins interact with E proteins in various combinations to form the various organ types [11]: sepals (A and E); carpels (CD and E); stamens (B, CD, and E); and petals (A, B, and E) [1,2,11-15]. Note that early researchers did not include E genes in sepals [16]. It is important to consider that E genes are involved in the formation of all floral organs [11], whereas AGL6 genes are involved primarily in the formation of the flower and cone in seed plants [13,17].

AGL6 and E genes present a high degree of sequence similarity and form sister clades in phylogenetic trees [13]. It has been reported that AGL6 genes in monocots and eudicots play an essential role in floral development [13,18]. The AGL6-like genes from grass form two paralogous clades: OsMADS17 and OsMADS6 [13,18]. The Arabidopsis genome contains two AGL6 genes (AGL6 and AGL13) [19], which suggests functional redundancy between the two genes.

Research into the origins of type II MADS-box genes has suggested that the B gene was the first to emerge [20–26]. The B/CD gene evolved relatively earlier than other flower identity genes [26]. However, related research has been unable to confirm the evolution order of AGL6/E/A gene. We used the ABCDE model (Fig 1) to estimate quantitatively the contribution of these genes to the development of floral organs. Furthermore, we performed detailed analysis of the ABCDE and AGL6 genes using the Circlize package in R (Fig 2).
Materials and methods

Searching species databases

As shown in S1 Table, data pertaining to ABCDE and AGL6 genes was obtained from the Arabidopsis thaliana Database (http://www.arabidopsis.org/) and Oryza sativa Database (http://rice.plantbiology.msu.edu/).

Building alignment and phylogenetic trees

The amino acid sequences were aligned using the program MUltiple Sequence Comparison by Log-Expectation (MUSCLE) for treeconstruction using the program MEGA6. Initial trees were constructed using the BEAST2.2 to construct Bayesian phylogenies [28]. The BEAST analysis was performed using a JTT substitution model and Yule priors-model. The stationary distribution of the MCMC chains and the convergence of runs were monitored using Tracer (v. 1. 6) to determine the appropriate MCMC chain length such that the effective sample size of every parameter was larger than 200 as recommended. Tree pictures were generated using

Fig 2. Example Circos plot created using the Circlize package in R, showing the contribution values of the ABCDE and AGL6 genes to floral organ development, as derived using Bayesian tree and ABCDE models. GV: Gradient values (the gradient value of the floral organs refers to the product of the importance values of floral organs and the ABCDE flower formation contribution value); ABCE:A+B+C+E; ALL:A+B+C+E+AGL6; BCE6:B+C+E+AGL6; ABE6: A+B+E+AGL6; BC:B+C; AB:A+B; BCE:B+C+E; ABE:A+B+E.

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TreeAnnotator (v. 1.8), with the first 1000 trees discarded as burn-in, and visualized using Figtree (v. 1.4) \cite{27}.

Circos plot

An initial plot was obtained using `circos.initialize` or `circos.initializeWithIdeogram` for the assignment of various categories of data to different sectors. We then used `circos`.

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Fig 3. Phylogeny of the ABCDE and AGL6 genes from *A. thaliana* and *O. sativa* and 31 classified protein sequences obtained using BEAST. The genes are indicated as follows: A gene, blue; B gene, green; CD gene, red; E gene, green; AGL6, pink. The Bayesian posterior probability values in tree. By using the BEAST tool, ABCDE and AGL6 genes appeared in the following order: B gene → CD gene → AGL6/E/A gene. The numbers 1, 2, 3 represent the order of evolution of ABCDE and AGL6 genes.

TreeAnnotator (v. 1.8), with the first 1000 trees discarded as burn-in, and visualized using Figtree (v. 1.4) \cite{27}.

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trackPlotRegion to create regions for the plotting of new tracks and the inclusion of basic graphics. When drawing multiple tracks, this second step is repeated before using Circos to generate the image [28].

Results and discussion

Phylogenetic analysis of the ABCDE and AGL6 genes

Bayesian methods were used to elucidate phylogenetic relationships (Fig 3) among the 31 sequences based on ABCDE and AGL6 protein sequences from *A. thaliana* and *O. sativa* (S1 Table). From Fig 3, the order of appearance was as follows: B gene → CD gene → AGL6/E/A gene. This result was followed to infer the contribution values of the ABCDE and AGL6 genes and the gradient values of the floral organs.

We employed the Bayesian evolutionary analysis by sampling trees (BEAST) program to construct a phylogenetic tree (Fig 3) for use in illustrating the evolutionary relationship among all of the ABCDE and AGL6 gene sequences. The Bayesian methods makes it possible to implement complex models of gene evolution [29].

The contribution values of the ABCDE and AGL6 genes

Assuming that the ABCDE genes contribute equally to flower formation, we assigned a flower formation contribution value of 1 unit for each of these genes. Thus, according to the ABCDE model (Fig 1), 2 units (A+E) contribute to sepal formation; 3 units (A+B+E) contribute to petal formation; 3 units (B+C+E) contribute to stamen formation; and 2 units (C+E) contribute to carpel formation. To maintain a maximum sum value of 1, the contribution values were adjusted as follows: sepals (A+E) = 0.2; petals (A+B+E) = 0.3; stamens (B+C+E) = 0.3; and carpels (C+E) = 0.2.

However, the contributions of the ABCDE genes should be adjusted based on the relative effects of their mutations on flower formation. As A gene mutants form only stamens and carpels [30], their flower formation contribution value is 0.5 (0.3+0.2), and their actual contribution value is 0.5 (1–0.5). As B gene mutants form only sepals and carpels [30], their flower formation contribution value is 0.4 (0.2+0.2), and their actual contribution value is 0.6 (1–0.4). As CD gene mutants form only sepals and petals [30], their flower formation contribution value is 0.5 (0.3+0.2), and their actual contribution value is 0.5 (1–0.5). Furthermore, as E gene mutants do not form flowers [30], therefore this gene has a flower formation contribution value of 1.0. According to the above assumptions, and given a maximum contribution sum value of 1, the flower formation contribution values of the ABCDE genes are as follows: A gene, 0.192; B gene, 0.231; CD gene, 0.192; and E gene, 0.385 (Table 1 and Fig 4).

The gradient values of the floral organs

Stamens produce pollen, which develops into male gametophytes [1]. Carpels develop in the center of the flower and produce ovules [1]. The presence of carpels unites angiosperms, making carpels the most important autapomorphy of the angiosperms [31]. The regenerative potential of stamens and carpels is only about half as high as that of petals [32]. Therefore, the regenerative ability of stamens and carpels is weaker, thereby increasing their importance. Sepals, which are sterile and green leaf-like organs, are the outermost organs of a flower (Fig 1), making them relatively unimportant.

Therefore, we were able to assume the relative importance of floral organs. From the innermost to outermost floral whorls, floral organs have relative importance values of 4 to 1. The assumption of this value is based on the reproductive importance of the flower and the
Table 1. The contribution values of the ABCDE and AGL6 genes.

|        | sepals | petals | stamens | carpels |
|--------|--------|--------|---------|---------|
| A      | 0.192  | 0.192  | 0       | 0       |
| B      | 0      | 0.231  | 0.231   | 0       |
| C      | 0      | 0      | 0.192   | 0.192   |
| E      | 0.385  | 0.385  | 0.385   | 0.385   |
| AGL6   | 0.077  | 0.077  | 0.077   | 0.077   |
| ABE    | 0.577  | 0.808  | 0.616   | 0.385   |
| BCE    | 0.385  | 0.616  | 0.808   | 0.577   |
| AB     | 0.192  | 0.421  | 0       | 0       |
| BC     | 0      | 0.231  | 0.423   | 0       |
| ABE6   | 0.654  | 0.885  | 0.693   | 0.462   |
| BCE6   | 0.462  | 0.693  | 0.885   | 0.654   |
| ALL    | 0.654  | 0.885  | 0.885   | 0.654   |
| ABCE   | 0.577  | 0.808  | 0.808   | 0.577   |

ABE: A+B+E, BCE: B+C+E, AB: A+B, BC: B+C, ABE6: A+B+E+AGL6, BCE6: B+C+E+AGL6, ALL: A+B+C+E+AGL6, ABCE: A+B+C+E.

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Fig 4. The contribution values of the ABCDE and AGL6 genes and the gradient values of the floral organs. The flower formation contribution values of the ABCDE genes are as follows: A gene, 0.192; B gene, 0.231; CD gene, 0.192; and E gene, 0.385. The gradient value of the floral organs refers to the product of the importance values of floral organs and the ABCDE flower formation contribution value. The gradient values of the floral organs: 0.572; petals, 1.606; stamens, 2.409; and carpels, 2.288.

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regenerative ability of floral organs. Carpels are located in the innermost layer of the flower and are relatively more important than stamens. Therefore, considering the relative importance values, we set carpels to 4 and stamens to 3. The more important consideration is that the regenerative potential of carpels is half that of the petals [32], so petals were set to 2. Thus, the value of the floral organs is as follows: carpels (CD+E), (0.192+0.385)\*4 = 2.288; stamens (B+CD+E), (0.231+0.192+0.385)\*3 = 2.409; petals (A+B+E), (0.192+0.231+0.385)\*2 = 1.606; and sepals (A+E), (0.192+0.385)\*1 = 0.572 (Table 1 and Fig 4). Such a value is called a gradient value. The gradient value of the floral organs refers to the product of the importance values of floral organs and the ABCDE flower formation contribution value. The higher the gradient value of the organ, the earlier in evolutionary history it emerged. In summary, our analysis indicates that floral organs emerged in the following sequence: stamens, → carpels, → petals, and → sepals. The stamens and carpels are the reproductive structures of angiosperms, whereas petals and sepals are supporting structures that may attract pollinators but are not essential for reproduction.

B genes are associated with the formation of petals and stamens (in angiosperms) as well as male cones (in gymnosperms) [33,34]. Male cones contain microsporophylls in which male gametophytes (pollen) are produced. Female cones contain megasporophylls on the surface of which develop ovules [14]. The fact that sporophylls are the gymnosperm structures most closely related to carpels means that angiosperm flowers and gymnosperm cones could be regarded as homologous [14]. In angiosperms, AGL6 genes are involved in flower development [13], whereas in gymnosperms, they are involved in cone formation [17]. Despite the fact that AGL6 and ABCDE genes play equally important roles in the formation of these structures, it is important to consider the evolutionary order of the constituent genes. In Fig 3, The B/CD gene evolved relatively earlier than other flower identity genes [26]. The flower formation contribution value of the B/CD genes is 0.423 (0.231+0.192).

Creating Circos plots of ABCDE and AGL6 genes using the Circlize package in R

Circlize (version 4.0.2) was used to visualize within a circular layout the contribution values of ABCDE and AGL6 genes in the context of floral organ development (Fig 2). Circos plots provide a basic template, which is easily modified with additional (higher-level) graphics focusing on specific details [28].

Using the analytic hierarchy process (AHP) to prove the contribution values and gradient values of floral organs

The analytic hierarchy process (AHP) is a multiple criteria decision-making tool applicable to almost any situation that involves decision-making [35]. In accordance with the methods described in How to make a decision: The Analytic Hierarchy Process [Saaty, 36], we employed the following derivation (Tables 2–7):

If the ratio of CI to that from random matrices is significantly small (specified at 10% or less), then we accept the estimate of w. Otherwise, we attempt to improve the consistency [35]. The CI in the current study was less than 0.1; therefore, we can infer that the contribution values of the floral organs are reasonable.

A/E/AGL6 genes arose through one of several possible evolutionary paths

AGL6 evolved first among the AGL6/E/A genes. The flower formation contribution of the ABCDE genes to angiosperm stamens and carpels is 0.5 (0.2+0.3), and the angiosperm
Table 2. W1-W6 value.

|            | Sepals | Petals | Stamens | Carpels |
|------------|--------|--------|---------|---------|
| Sepals     | 1      | W1     | W2      | W3      |
| Petals     | $\frac{1}{W1}$ | 1    | W4      | W5      |
| Stamens    | $\frac{1}{W2}$ | $\frac{1}{W1}$ | 1      | W6      |
| Carpels    | $\frac{1}{W3}$ | $\frac{1}{W1}$ | $\frac{1}{W1}$ | 1      |

$W_n = \sqrt{W1 \times W2}$

W1 (Sepals-Petals) = $\sqrt{0.572 \times 0.606} = 0.9584$.

W2 (Sepals-Stamens) = $\sqrt{0.572 \times 2.409} = 1.1738$.

W3 (Sepals-Carpels) = $\sqrt{0.572 \times 2.288} = 1.1440$.

W4 (Petals-Stamens) = $\sqrt{1.606 \times 2.409} = 1.9669$.

W5 (Petals-Carpels) = $\sqrt{1.606 \times 2.288} = 1.9169$.

W6 (Stamens-Carpels) = $\sqrt{2.409 \times 2.288} = 2.3477$.

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Table 3. Sum of W1-W6 value.

|            | Sepals | Petals | Stamens | Carpels |
|------------|--------|--------|---------|---------|
| Sepals     | 1      | 0.9584 | 1.1738  | 1.1440  |
| Petals     | 1.0434 | 1      | 1.9669  | 1.9169  |
| Stamens    | 0.8519 | 0.5084 | 1       | 2.3477  |
| Carpels    | 0.8741 | 0.5216 | 0.4259  | 1       |
| Sum        | 3.7694 | 2.9884 | 4.5666  | 6.4086  |

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Table 4. A value divided by the sum.

|            | Sepals | Petals | Stamens | Carpels |
|------------|--------|--------|---------|---------|
| Sepals     | $\frac{1}{1.1738} = 0.2652$ | $\frac{0.9584}{1} = 0.9584$ | $\frac{1.1738}{1} = 1.1738$ | $\frac{1.1440}{1} = 1.1440$ |
| Petals     | $\frac{1}{2.409} = 0.2768$ | $\frac{1}{1} = 1$ | $\frac{1.9669}{1} = 1.9669$ | $\frac{1.9169}{1} = 1.9169$ |
| Stamens    | $\frac{1}{2.288} = 0.2260$ | $\frac{0.5084}{1} = 0.5084$ | $\frac{1}{1} = 1$ | $\frac{2.3477}{1} = 2.3477$ |
| Carpels    | $\frac{1}{2.228} = 0.2319$ | $\frac{0.4259}{1} = 0.4259$ | $\frac{0.4259}{1} = 0.4259$ | $\frac{1}{1} = 1$ |

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Table 5. V value.

|            | V value |
|------------|---------|
| Sepals     | $\frac{0.2032 - 0.1207 - 0.2570 + 0.1785}{11} = 0.2554$ |
| Petals     | $\frac{0.2758 - 0.1346 - 0.4372 + 0.2913}{11} = 0.3353$ |
| Stamens    | $\frac{0.2680 - 0.1701 - 0.2139 + 0.3952}{11} = 0.2554$ |
| Carpels    | $\frac{0.2170 - 0.1731 - 0.0901 + 0.1502}{11} = 0.1639$ |

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flowers and gymnosperm cones are homologous structures. The B/CD/AGL6 genes and stamens and carpels evolved first; therefore, B+CD+AGL6 = 0.5 and the contribution value of the AGL6 gene is 0.077 (0.5–0.231–0.192). Although AGL6 does not directly influence floral organ development, it is critical for the reproductive abilities of both gymnosperms and angiosperms [13,17]. Thus, it is not surprising that AGL6 contributes less value to flower formation than do the ABCDE genes. The approach used here is one way to estimate the flower formation contribution value of AGL6; however, because AGL6 does not directly influence floral structures, it is difficult to determine its flower formation contribution value.

a) The B/CD/AGL6 genes evolved soon after the E genes.

As the B/CD/AGL6/E genes were available, flowers formed petals, stamens, and pistils, but not sepals.

b) The B/CD/AGL6 genes evolved soon after the A genes.

As only the B/CD/AGL6/A genes were available, flowers could form due to the lack of the E gene. Therefore, a reasonable evolutionary order is B genes→CD genes→AGL6→E genes→A genes. AGL6 and E genes have a high degree of sequence similarity and form sister clades in phylogenetic trees [32]. Another possible evolutionary order is: B genes→CD genes→AGL6/E genes→A genes.

The E genes evolved first among the AGL6/E/A genes

a) The B/CD/E genes evolved soon after the AGL6 gene.

As B/CD/E/AGL6 genes were available, flowers formed stamens and pistils, but still lacked the A gene needed for sepals and petals.

Table 7. [A] × [V]/[V].

|       | [A] × [V]/[V] |
|-------|---------------|
| Sepals | 4.1664        |
| Petals | 4.2299        |
| Stamens| 4.0262        |
| Carpels| 4.0927        |

* Average value (λ): \( \frac{\frac{4.1664 + 4.2299 + 4.0262 + 4.0927}{4}}{4} = 4.1288 \).

CI (consistency index) = \( \frac{4}{4-1} = \frac{4.1288 - 4}{4-1} = 0.0429 \).
b) The B/CD/E genes evolved soon after the A genes.

The presence of B/CD/E/A genes, but the absence of AGL6, may have resulted in defective flower development. Therefore, it is unlikely that the E genes evolved first among the AGL6/E/A genes.

The A gene evolved first among the AGL6/E/A genes. In the absence of E and AGL6 genes, flower formation would not have been possible. Therefore, it is unlikely that the A gene evolved first among the AGL6/E/A genes.

Conclusions

We use the analytic hierarchy process (AHP) to prove the contribution values and gradient values of floral organs. This is the first paper to understand contribution values of ABCDE and AGL6 genes using the AHP. According to the proposed ABCDE model (Fig 1), the flower formation contribution values of the ABCDE and AGL6 genes are as follows: A gene, 0.192; B gene, 0.231; CD gene, 0.192; E gene, 0.385; and AGL6, 0.077 (Fig 4). Furthermore, the following gradient values of the floral organs were calculated: sepals, 0.572; petals, 1.606; stamens, 2.409; and carpels, 2.288 (Fig 4). The gradient value of the floral organs refers to the product of the importance values of floral organs and the ABCDE flower formation contribution value. Floral organs with a higher gradient value emerged earlier in evolutionary history. Hence, our analysis suggests that the order in which the floral organs evolved was stamens, carpels, petals, and then sepals. Additionally, the ABCDE and AGL6 genes may have emerged in the following order: B genes → CD genes → AGL6 → E genes → A genes. Another possible evolutionary order is B genes → CD genes → AGL6/E genes → A genes. We also performed detailed analysis of the ABCDE and AGL6 genes using the Circlize package in R (Fig 2). This is the first study to use Circos plots of ABCDE and AGL6 genes using the Circlize package in R. This research provides a refined model for floral organ evolution that can be used to explore the emergence of floral organs and the origin of the MADS-box genes.

Supporting information

S1 Table. The homeotic gene classification of Arabidopsis thaliana and Oryza sativa. (DOCX)

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Author Contributions

Formal analysis: Gangxu Shen.
Methodology: Gangxu Shen.
Supervision: Wei-Lung Wang.
Writing – original draft: Gangxu Shen.

References

1. Krizek BA, Fletcher JC (2005) Molecular mechanisms of flower development: an armchair guide. Nat Rev Genet 6(9): 688–98. https://doi.org/10.1038/nrg1675 PMID: 16151374
2. Urbanus SL, de Folter S, Shchennikova AV, Kaufmann K, Immink RGH, Angenent GC (2009) In planta localisation patterns of MADS domain proteins during floral development in Arabidopsis thaliana. BMC Plant Biol 9(1):5. https://doi.org/10.1186/1471-2229-9-5 PMID: 19138429

3. Murai K (2013) Homeotic Genes and the ABCDE Model for Floral Organ Formation in Wheat. Plants 2 (3): 379–95. https://doi.org/10.3399/plants2030379 PMID: 27137382

4. Paříčková L, de Folter S, Kieffer M, Horner DS, Favalli C, Busscher J, et al. (2003) Molecular and Phylogenetic Analyses of the Complete MADS-Box Transcription Factor Family in Arabidopsis. Plant Cell 15(7): 1538–51. https://doi.org/10.1105/tpc.011544 PMID: 12837945

5. Jiang S-C, Pang C-Y, Song M-Z, Wei H-L, Fan S-L, Yu S-X (2014) Analysis of MiKC6−→type MADS-box gene family in Gossypium hirsutum. J Integr Agr 13(6): 1239–49.

6. Gramzow L, Ritz MS, Theißen G (2010) On the origin of MADS-domain transcription factors. Trends Genet 26(4): 149–53. https://doi.org/10.1016/j.tig.2010.01.004 PMID: 20219261

7. Theisssen G, Kim JT, Saedler H (1996) Classification and phylogeny of the MADS-box multigene family suggest defined roles of MADS-box gene subfamilies in the morphological evolution of eukaryotes. J Mol Evol 43(5): 484–516. https://doi.org/10.1007/BF02337521 PMID: 8875863

8. Kaufmann K, Melzer R, Theißen G (2005) MiKC-type MADS-domain proteins: structural modularity, protein interactions and network evolution in land plants. Gene 347(2): 183–98. https://doi.org/10.1016/j.gene.2004.12.014 PMID: 15777618

9. Gramzow L, Theißen G (2010) A hitchhiker’s guide to the MADS world of plants. Genome Biol 11(6): 1–11.

10. Dreni L, Zhang D (2016) Flower development: the evolutionary history and functions of the AGL6 subfamily MADS-box genes. J Exp Bot 67(6): 1625–38. https://doi.org/10.1093/jxb/erw046 PMID: 26956504

11. Wellmer F, Graci et E, Riechmann JL (2014) Specification of floral organs in Arabidopsis. J Exp Bot 65 (1): 1–9. https://doi.org/10.1093/jxb/ert35 PMID: 24277279

12. Kim S, Koh J, Yoo MJ, Kong H, Hu Y, Ma H, et al. (2005) Expression of floral MADS-box genes in basal angiosperms: Implications for the evolution of floral regulators. Plant J 43(5): 724–44. https://doi.org/10.1111/j.1365-313X.2005.02487.x PMID: 16115069

13. Li H, Liang W, Hu Y, Zha L, Yin C, Xu J, et al. (2011) Rice MAD6S Interacts with the Floral Homeotic Genes SUPERWOMAN1, MAD3, MAD58, MAD313, and DROOPING LEAF in Specifying Floral Organ Identities and Meristem Fate. Plant Cell 23(7): 2536–52. https://doi.org/10.1105/tpc.111.087262 PMID: 21784949

14. Ó’Maoiléidigh DS, Graci et E, Wellmer F (2013) Genenetworks controlling Arabidopsis thaliana flower development. New Phytol 199(1): 16–30. https://doi.org/10.1111/nph.12444 PMID: 23952532

15. Yuan Z, Zhang D (2015) Roles of jasmonate signalling in plant inflorescence and flower development. Curr Opin Plant Biol 27: 44–51. https://doi.org/10.1016/j.pbi.2015.05.024 PMID: 26125498

16. Kramer EM, Hall JC (2005) Evolutionary dynamics of genes controlling floral development. Curr Opin Plant Biol 8(1): 13–8. https://doi.org/10.1016/j.pbi.2004.09.019 PMID: 15653394

17. Katahata S-I, Futamura N, Igasaki T, Shinohara K (2014) Functional analysis of SOC1-like and AGL6-like MADS-box genes of the gymnosperm Cryptomeria japonica. Tree Genet Genomes 10(2): 317–27.

18. Ohmori S, Kimizu M, Sugita M, Miyao A, Hirochika H, Uchida E, et al (2009) MOSAIC FLORAL ORGAN51 an AGL6-like MADS box gene, regulates floral organ identity and meristem fate in rice. Plant Cell 21: 3008–3025. https://doi.org/10.1105/tpc.109.068742 PMID: 19820190

19. Vandenbussche MG, Van de Peer Y, Gerats T (2003) Structural diversification and neo-functionalization during floral MADS-box gene evolution by C-terminal frameshift mutations. Nucleic Acids Res 31: 4401–4409. https://doi.org/10.1093/nar/gkg642 PMID: 12888499

20. Becker A, Winter K-U, Meyer B, Saedler H, Theißen G (2000) MADS-box gene diversity in seed plants 300 million years ago. Mol Phylogenet Evol 17(10): 1425–34. https://doi.org/10.1016/s1050-7998(00)00207-0 PMID: 11018150

21. Becker A, Theißen G (2003) The major clades of MADS-box genes and their role in the development and evolution of flowering plants. Mol Phylogenet Evol 20(3): 464–89. https://doi.org/10.1016/s1055-7903(03)00207-0 PMID: 14615187

22. De Bodt S, Raes J, Van de Peer Y, Theißen G (2003) And then there were many: MADS goes genomic. Trends Plant Sci 8(10): 4401–4409. https://doi.org/10.1016/j.tplants.2003.09.006 PMID: 14557044

23. Nam J (2003) Antiquity and Evolution of the MADS-Box Gene Family Controlling Flower Development in Plants. Mol Biol Evol 20(8): 1435–47. https://doi.org/10.1093/molbev/msg152 PMID: 12777513

24. Hernandez-Hernández T, Martinez-Castilla LP, Alvarez-Buylla ER (2007) Functional diversification of B MADS-box homeotic regulators of flower development: adaptive evolution in protein–protein interaction
domains after major gene duplication events. Mol Biol Evol 24(2): 465–81. https://doi.org/10.1093/molbev/msl182 PMID: 1713533

25. Airoldi CA, Davies B (2012) Gene duplication and the evolution of plant MADS-box transcription factors. J Genet Genomics 39(4): 157–65. https://doi.org/10.1016/j.jgg.2012.02.008 PMID: 22546537

26. Shen G, Yang C-H, Shen C-Y, Huang K-S (2019) Origination and selection of ABCDE and AGL6 sub-family MADS-box genes in gymnosperms and angiosperms. Biol Res 52(1): 1–15. https://doi.org/10.1186/s40659-018-0209-0 PMID: 30612577

27. Bouckaert R, Heled J, Kühnert D, Vaughan T, Wu C-H, Xie D, et al. (2014) BEAST 2: a software platform for Bayesian evolutionary analysis. PLoS Comput Biol 10(4): e1003537. https://doi.org/10.1371/journal.pcbi.1003537 PMID: 24722319

28. Gu Z, Gu L, Els R, Schlesner M, Brors B (2014) Circleviz implements and enhances circular visualization in R. Bioinformatics 30(19): 2811–2. https://doi.org/10.1093/bioinformatics/btu393 PMID: 24930139

29. Kater MM, Dreni L, Colombo L (2006) Functional conservation of MADS-box factors controlling floral organ identity in rice and Arabidopsis. J Exp Bot 57(13): 3433–44. https://doi.org/10.1093/jxb/erl097 PMID: 16968881

30. Pfannebecker KC, Lange M, Rupp O, Becker A (2016) An Evolutionary Framework for Carpel Developmental Control Genes. Mol Biol Evol msw 229.

31. Wojciechowicz MK (2007) Comparison of regenerative potential of petals, stamens and pistils of five Sedum species in vitro. Biodiv Res Conserv 5–8: 87–94.

32. Sundström J, Carlsbecker A, Svensson ME, Svensson M, Johanson U, Theißen G, et al. (1999) MADS-box genes active in developing pollen cones of Norway spruce (Picea abies) are homologous to the B-class floral homeotic genes in angiosperms. Dev Genet 25(3): 253–66. https://doi.org/10.1002/(SICI)1520-6408(1999)25:3<253::AID-DVG8>3.0.CO;2-P PMID: 10528266

33. Winter K-U. Becker A, Münster T, Kim JT, Saedler H, Theissen G (1999) MADS-box genes reveal that gnetophytes are more closely related to conifers than to flowering plants. Proc Natl Acad Sci USA 96(13): 7342–7. https://doi.org/10.1073/pnas.96.13.7342 PMID: 10377416

34. Albert VA, Barbazuk WB, Depamphilis CW, Der JP, Leebeens-Mack J, Ma H, et al. (2013) The Amborella genome and the evolution of flowering plants. Science 342(6165): 1241089. https://doi.org/10.1126/science.1241089 PMID: 24357323

35. Vaidya OS, Kumar S (2016) Analytic hierarchy process: An overview of applications. Eur J Oper Res 169: 1–29.

36. Saaty TL (1990) How to make a decision: The Analytic Hierarchy Process. Eur J Oper Res 48: 9–26.