



Contents lists available at ScienceDirect

Seminars in Cell & Developmental Biology

journal homepage: www.elsevier.com/locate/semcdb



Review

Evolvability of flower geometry: Convergence in pollinator-driven morphological evolution of flowers

Natalia Joanna Woźniak, Adrien Sicard*

Institut für Biochemie und Biologie, Universität Potsdam, Karl-Liebknecht-Str. 24-25, 14476 Potsdam-Golm, Germany

ARTICLE INFO

Article history:

Received 24 May 2017
Received in revised form
18 September 2017
Accepted 19 September 2017
Available online xxx

Keywords:

Flower
Developmental evolution
Morphogenesis
Angiosperms
Co-evolution
Plant-pollinator interactions

ABSTRACT

Flowers represent a key innovation during plant evolution. Driven by reproductive optimization, evolution of flower morphology has been central in boosting species diversification. In most cases, this has happened through specialized interactions with animal pollinators and subsequent reduction of gene flow between specialized morphs. While radiation has led to an enormous variability in flower forms and sizes, recurrent evolutionary patterns can be observed. Here, we discuss the targets of selection involved in major trends of pollinator-driven flower evolution. We review recent findings on their adaptive values, developmental grounds and genetic bases, in an attempt to better understand the repeated nature of pollinator-driven flower evolution. This analysis highlights how structural innovation can provide flexibility in phenotypic evolution, adaptation and speciation.

© 2017 Elsevier Ltd. All rights reserved.

Contents

1. Introduction.....	00
2. Morphological innovation.....	00
2.1. Evolution of flower symmetry.....	00
2.1.1. The role of flower symmetry in pollination specialization.....	00
2.1.2. Genetic basis of the repeated shift in flower symmetry.....	00
2.2. Limiting the access to rewards to specific pollinators.....	00
2.2.1. Synorganization, organ fusion and the evolution of sympetaly.....	00
2.2.2. Flower spur evolution.....	00
3. Quantitative changes in flower geometry.....	00
3.1. Floral tube and nectar spur length.....	00
3.2. Evolution of the anther-style length ratio.....	00
3.3. Flower size evolution.....	00
3.4. Variation of organ shape.....	00
3.5. Change in organ numbers.....	00
4. Conclusion and perspectives.....	00
Acknowledgements.....	00
References.....	00

* Corresponding author.

E-mail address: adrien.sicard@uni-potsdam.de (A. Sicard).

1. Introduction

With approximately 350 000 species identified so far angiosperms (or flowering plants), account for nearly 90% of all known plant species [1,2]. Interestingly, this is also the youngest plant group, with recent age estimates of the crown node ranging between 251 and 192 MYA [3]. The emergence of angiosperms has, therefore, been followed by a rapid and extensive species radiation starting in the Early Cretaceous [4–6] and accompanied by an astonishing diversification of flower structures and forms. Together, these observations suggest that the flower constitutes a key evolutionary innovation and that the evolution of its morphology has since played a central role in promoting speciation.

Flowers are, typically, composed of a succession of four organs: the sepals (the outermost leaf-like protective structures), the petals (colourful organs mostly involved in pollinator attraction), the stamens (male reproductive organs) and at the centre the carpels (female reproductive organs). Their structure vary, however, enormously within the angiosperms with respect to: the number of the four primary floral organs, the arrangement of these organs within the flowers (i.e. phyllotaxis where spiral, whorled or irregular arrangements can be found) as well as their shapes and dimensions [5–15].

Changes in flower morphology are thought to evolve as adaptations for improved reproductive efficiency in different modes of pollination [16,17]; but also in different mating systems [18]. Since 87.5% of the angiosperm species are animal-pollinated [19], it is generally accepted that the coevolution between plants and their pollinators has been the major evolutionary force driving the rapid diversification of angiosperms [4,20–23]. This is supported by the co-diversification of some insects, birds and mammals in the same period and by the observation that divergent pollinator-driven selection lead to divergent evolution in plant traits [17,23–25]. By leading to reproductive isolation and speciation, the specialization to different pollinators appears to have promoted species diversification and morphological evolution [16,26,27]. Nevertheless, specialization of evolutionary unrelated angiosperm taxa to similar pollinators resulted, in many instances, in convergent evolution of specific combinations of floral traits (shape, size, colour, scent, reward, etc.), also known as pollination syndromes [28,29]. The original concept of highly specialized interactions in the notion of pollination syndromes has, however, been challenged by the observation that flowers are often visited by a wide range of pollinator species. Stebbins (1970) [16] proposed that pollination syndrome evolved to increase pollen transfer by the most effective and/or abundant pollinators, while decreasing the rate of visitation by floral antagonists. Later studies clustered pollinators into functional groups (i.e. that have similar phenotypes as well as behaviour and exert similar selective pressures on floral traits) and successfully identified floral syndromes associated with particular groups [29]. Several studies have, since, attempted to test the notion of pollination syndrome by determining to which extent flower phenotypes allow to predict the most effective pollinators [30–36]. The contrasting results obtained by these studies have left a, still, unresolved debate on the use of pollination syndrome as a predictive tool [29–31,37–39]. It appears, however, clear that pollination syndrome is not an universal concept and that other selective agents act in conjunction with or independently from pollinators to drive the evolution of flower morphology [39]. Nevertheless, the phenotypic convergence often observed in independent adaptations to similar pollinators suggests an intimate relationship between flower morphology and pollination efficiency and/or the existence of conserved genetic limitations to reach an optimum fitness in different plant-pollinator interactions [40,41].

The structure of the genetic networks controlling developmental traits may, indeed, have a profound influence on the target of

evolution [42]. Within these networks, genes with low pleiotropy and high phenotypic effect, such as input/output genes mediating between upstream patterning factors and downstream growth regulators, appear more 'suitable' for evolutionary changes and, thus, more likely to underlie convergent evolution [43–45]. Evolutionary reuse of such 'central node' genes in the genetic network controlling floral traits, i.e. repeated independent mutations in the same gene, may explain, at least in part, the phenotypic convergence observed in independent adaptations to similar pollinators. The molecular nature of evolutionary novelty has been actively debated [42,46,47]. It appears, nevertheless, clear from empirical data that regulatory changes in gene expression has a central role in developmental evolution. These changes may result from *cis*-regulatory and/or coding mutations leading to the reshuffling of existing gene networks. Gene duplication also play an important role in evolution by providing new genetic material from which new functions can evolve through the divergence of the newly duplicated gene copies, i.e. paralogs [48]. Whole Genome Duplication (WGD) is likely to have played a determinant role in the flower morphology radiation in angiosperms. Indeed, several WGD appeared to precede radiation events within different angiosperm lineages and transcriptional regulators seem to have been preferentially retained after these events (see [49] for review). Gene duplications and the subsequent functional diversification of paralogs, may have, therefore, allowed the expansion of the genetic tool sets on which evolutionary processes could act and in turn, permitted a rapid diversification and complexification of flower structures. Despite the flexibility that gene duplication may confer to phenotypic evolution, similar adaptive morphological solutions have evolved to similar ecological challenges with often the co-option of similar gene regulatory networks (GRNs) [50].

In this review, we will describe the major trends of pollinator-driven morphological evolution of flowers, their ecological context and genetic basis, with a focus on studies that documented phenotypic selection on flower shape and size in the eudicots in particular. Finally, we will also attempt to assess the level of molecular convergence and discuss the repeated nature of specific changes with regards to their adaptive values and the complexity of their underlying GRNs. We discuss, here, only the major flower morphs but it is to note that flower diversity is such that these categories are often not absolutes.

2. Morphological innovation

2.1. Evolution of flower symmetry

2.1.1. The role of flower symmetry in pollination specialization

The arrangement of organs within the flower may create a variable number of symmetry planes along which the flower can be divided into identical mirror images or "flower segments". Flowers can be radially symmetrical (where several mostly identical flower segments occur regularly around the stem axis), dissymmetrical (with two perpendicular planes of symmetry), bilaterally symmetrical (with only one symmetry plane) or totally asymmetrical (Fig. 1) [51,52]. The symmetry of the flower is mostly influenced by the regulation of organ positioning and growth pattern within the flower. For instance, in radially symmetrical flowers all organs of the same type within each whorl have roughly the same size and shape as their counterparts around the flower stem axis. Bilaterally symmetrical flowers have only one symmetry axis, often because of an uneven growth between the adaxial (i.e. dorsal) and abaxial (i.e. ventral) half of the flowers [53]. Transition in flower symmetry and in particular toward bilateral symmetry is one of the major evolutionary trends during the diversification of angiosperms. Indeed, Reyes et al. (2016) have recently estimated that there were almost

Download English Version:

<https://daneshyari.com/en/article/8479571>

Download Persian Version:

<https://daneshyari.com/article/8479571>

[Daneshyari.com](https://daneshyari.com)