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Towards a comprehensive and dynamic gynoecium gene regulatory network

Ricardo A. Chávez Montes, Humberto Herrera-Ubaldo, Joanna Serwatowska, Stefan de Folter*

Unidad de Genómica Avanzada (LANGEBIO), Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional (CINVESTAV-IPN), Km. 9.6 Libramiento Norte, Carretera Irapuato-León, CP 36821 Irapuato, Guanajuato, Mexico

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ABSTRACT

The *Arabidopsis thaliana* gynoecium arises at the center of the flower as a simple structure, which will successively develop novel cell types and tissues, resulting in a complex organ. Genetic and hormonal factors involved in this process have been identified, but we are still far from understanding how these elements interact, and how these interactions rearrange according to spatial and temporal cues. In this work we propose the first steps in a roadmap to attain an ambitious goal: to obtain a comprehensive and dynamic gene regulatory network that will help us elucidate the patterning events leading to the formation of a fully developed gynoecium.

1. Introduction

In flowering plants the gynoecium is the female reproductive organ, which is composed either of a single carpel, or multiple carpels that are usually fused. The gynoecium of *Arabidopsis thaliana* is composed of two carpels fused along their margins. This fusion zone, called medial ridge or carpel margin meristem (CMM), acts as meristematic tissue giving rise to internal structures such as placenta, ovules, replum, septum and transmitting tract [1,2]. According to the floral development stages described by Smyth and collaborators [3], the gynoecium is clearly established at stage 6, when the spatial domains of the gynoecial tube become visible. These include the medial domain versus the lateral domains, and the inner (adaxial) and outer (abaxial) regions. Later, during stages 7–8, two meristematic outgrowths (CMMs) form at the inner medial domain, which subsequently (stages 9–12) will produce key reproductive tissues: placenta, ovules and transmitting tract. A schematic representation of gynoecium inner tissues development from stages 8 to 12 is shown in Fig. 1a. At anthesis, by stage 12, all tissues required for fertilization, and the following fruit development are present. The former are fully developed, while the latter will develop after fruit set [4,5]. The fully developed, stage 12 gynoecium is composed of three distinct structures along the apical-basal axis: stigma, style and ovary (Fig. 1b).

Several genetic and hormonal factors that participate in gynoecium development have been identified (reviewed in [2]), but we are still far from understanding how all these elements interact to give rise to the morphogenetic patterns we observe. Available genome-wide analyses in other organs, such as roots or the shoot apical meristem, have revealed that developmental processes are controlled by the coordinated action of regulators, that is gene regulatory networks (GRNs), that control gene expression according to spatial and temporal cues [6–8]. These networks are composed of transcription factors, hormones, microRNAs, peptides and chromatin-modifying proteins, together with their interactions, in particular protein-DNA and protein–protein interactions. For gynoecia, a few, small GRNs have been proposed for specific cell types (Fig. 2). However, we are still far from obtaining a definitive, comprehensive gynoecium GRN, and understanding how it evolves in a spatio-temporal context. In this review we propose the first steps in a roadmap to attain such goal, with a particular emphasis on transcription factors, and their protein-DNA and protein–protein interactions.

2. Identifying gynoecium expressed genes

The first cloned gene involved in gynoecium development, *AGAMOUS* (*AG*), was described in 1990, 25 years ago [9]. Since then, dozens of genes have been identified and, in a recent review, Reyes-

Abbreviations: GRN, gene regulatory network; TF, transcription factor; ChIP, chromatin immunoprecipitation; TRAP, translating ribosome affinity purification; PBM, protein binding microarray.

* Corresponding author.
E-mail address: sdfolter@langebio.cinvestav.mx (S. de Folter).

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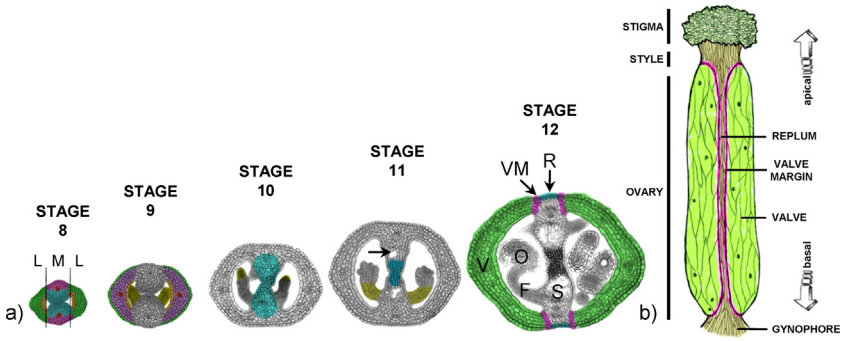

Fig. 1. *Arabidopsis thaliana* carpel tissues development. (a) False-colored histological cross sections of Arabidopsis gynoecia from stages 8 to 12 (accession Col-0). Stage 8 gynoecium: the medial domain (M) is observable, composed of the carpel margin meristem (blue) and the abaxial margin or replum zone (pink). Main vascular bundles differentiate at this stage (red). Lateral domains (L) are divided morphologically into inner (adaxial, orange) and outer (abaxial, green) regions. Stage 9: carpel wall differentiates into three tissues: exocarp (green), mesocarp (purple) and endocarp (orange). Lateral vascular bundles differentiate (red) and ovule primordia begin to form (yellow). Stage 10: the medial ridges meet and give rise to the septum (blue). Ovules differentiate (yellow). Stage 11: the transmitting tract differentiates (blue), and cell death begins in the septum (arrow). Stage 12 (anthesis): valve margins (VM, pink) and replum (R, blue) become morphologically distinct from the valves (V, green). Funiculus (F) and ovules (O) are fully developed. (b) Cartoon representation of a stage 12 wild type *Arabidopsis* gynoecium showing the different tissues that can be distinguished along the apico-basal axis: stigma, style, ovary and gynophore.

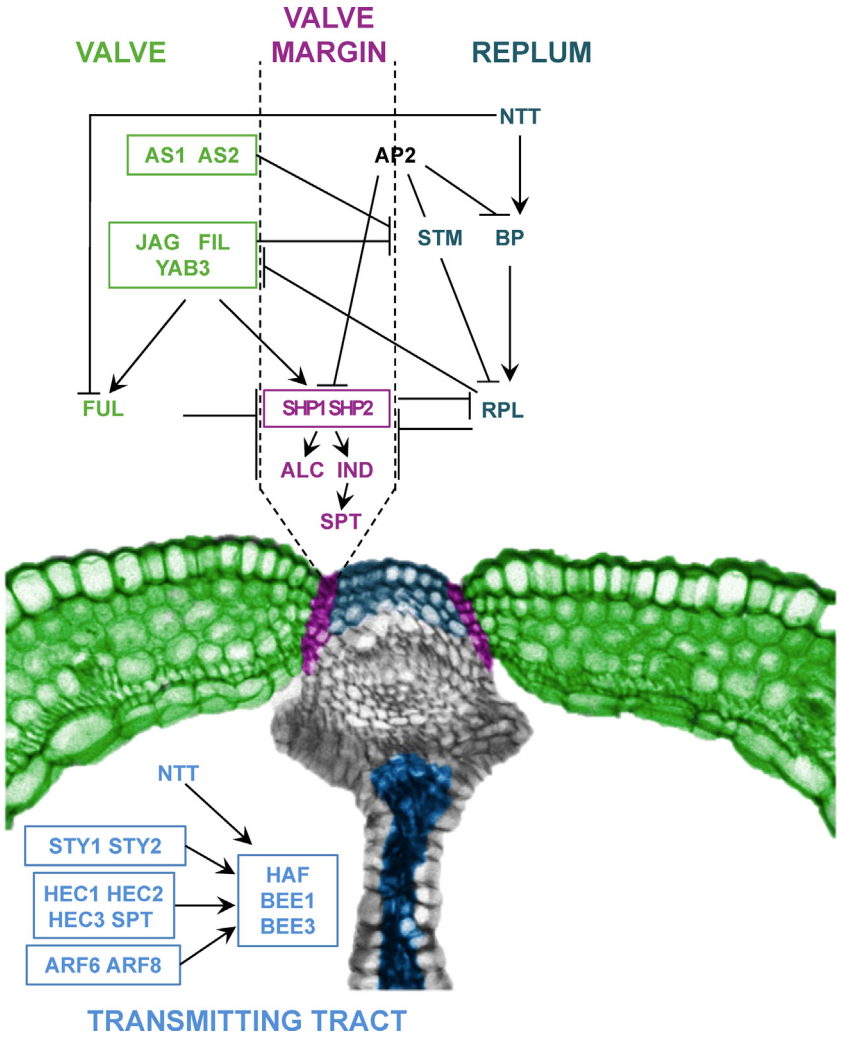

Fig. 2. Known gynoecium GRNs for valve, valve margin, replum and transmitting tract. *Arabidopsis thaliana* (ecotype Col-0) fruit false-colored histological cross section showing the valve, valve margin, replum and transmitting tract region. The corresponding GRNs are displayed in the same color as the tissues they specify. Functionally redundant genes are boxed. Specification along the medial-lateral axis is the result of the antagonistic activities of lateral factors (*ASYMMETRIC LEAVES 1* and *2*, *AS1,2*; *JAGGED*, *JAG*; *FILAMENTOUS FLOWER*, *FIL*; *YABBY3*, *YAB3*; *FRUITFULL*, *FUL*) and medial factors (*NO TRANSMITTING TRACT*, *NTT*; *SHOOT MERISTEMLESS*, *STM*; *BREVIPEDICELLUS*, *BP*; *REPLUMLESS*, *RPL*). Differentiation of the valve margin, controlled by *SHATTERPROOF 1* and *2* (*SHP1*, *2*), *ALCATRAZ* (*ALC*), *INDEHISCENT* (*IND*) and *SPATULA* (*SPT*), is regulated by both lateral and medial factors. *APETALA 2* (*AP2*) is involved in valve margin and replum specification, and is expressed in both tissues. Several genes are known to participate in transmitting tract development (*STYLISH 1* and *2*, *STYs*; *HECATE 1*, *2* and *3*, *HEC1,2,3*; *SPT*; *AUXIN RESPONSE FACTOR 6* and *8*, *ARF6*, *8*; *HALF FILLED*, *HAF*; *BR ENHANCED EXPRESSION 1* and *3*, *BEE1*, *3*; *NTT*), but the underlying GRN has not been fully elucidated. *NTT* was first described as an essential gene for transmitting tract formation and, more recently, was also shown to promote replum development. The presented GRNs were reconstructed according to [5,16,55,86–89].