



# Developmental cartography: coordination via hormonal and genetic interactions during gynoecium formation

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Development in multicellular organisms requires the establishment of tissue identity through polarity cues. The *Arabidopsis* gynoecium presents an excellent model to study this coordination, as it comprises a complex tissue structure which is established through multiple polarity systems. The gynoecium is derived from the fusion of two carpels and forms in the centre of the flower. Many regulators of carpel development also have roles in leaf development, emphasizing the evolutionary origin of carpels as modified leaves. The gynoecium can therefore be considered as having evolved from a simple setup followed by adjustment in tissue polarity to facilitate efficient reproduction. Here, we discuss concepts to understand how hormonal and genetic systems interact to pattern the gynoecium.

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## Introduction

A common aspect of multicellular organism development is the function of morphogens to guide cellular patterning of complex organs [1]. In the plant kingdom, the role of a morphogen is often attributed to hormones, however, plant organ morphogenesis is not possible without the interplay of hormonal signalling and transcription factor systems.

In flowering plants (Angiosperms), the female reproductive organ, the gynoecium, develops from carpels at the centre of the flower. Studies in the model plant, *Arabidopsis*, show that gynoecium formation depends on the output of precise hormonal and genetic interactions in order to establish its complex tissue organization [2,3]. The gynoecium comprises several tissue domains, each with very specific functions, and can be described along

different morphological axes of polarity [4,5]. Along the apical-basal axis, the stigma, style, ovary and gynophore develop. Externally along medio-lateral axis are found the replum, valve margins and valves (carpel walls), while internally the transmitting tract, septum and ovules are formed (Figure 1). An abaxial-adaxial polarity axis forms across the valves (Figure 1); however, in this review we will focus on establishing the apical-basal and medio-lateral axes as these are most prominent in the formation of the overall gynoecium structure.

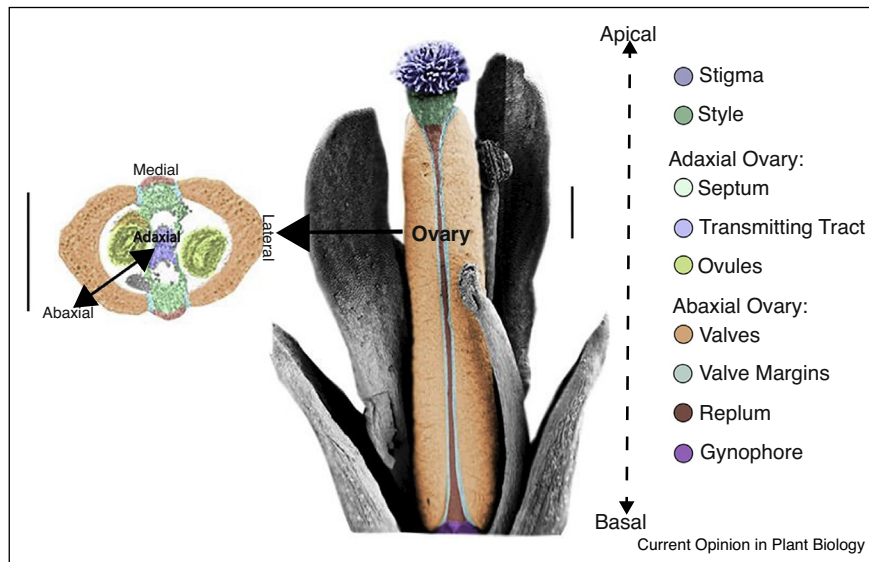
While great progress has been made in the last decade in understanding transcriptional circuits and their feedback mechanisms with hormones to pattern the gynoecium, we still do not have a complete picture as to how these elements orchestrate the development of the organ as a whole. This review explores the concepts that will contribute to our understanding of how hormonal and genetic systems work in a coordinating fashion to pattern the gynoecium.

## Laying down the foundations: hormonal boundaries in the gynoecium

The pivotal role of auxin in gynoecium development was first described by treating *Arabidopsis* gynoecia with the polar auxin transport inhibitor naphthylphthalamic acid (NPA) resulting in severe patterning defects [6]. Since then, mutants in auxin biosynthesis, polar auxin transport and signalling have been shown to display defects in both apical-basal and medio-lateral polarity establishment [7,8,9]. These defects include variability in the size of the valves and over-developed medial tissues [6,10].

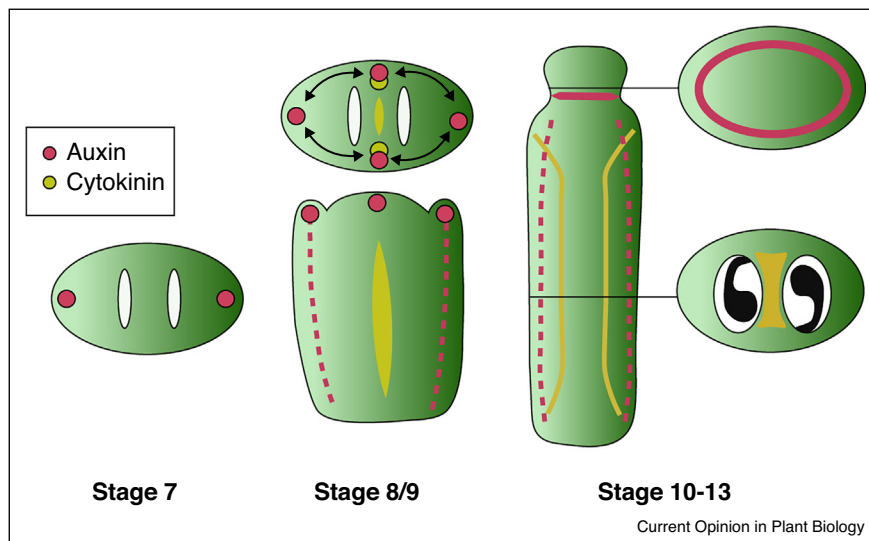
Auxin signalling reporter lines such as *DR5::GFP* [11] and *DII-VENUS* [12] have since facilitated studies to coordinate pattern specification with auxin distribution [8,13,14,15]. At stage 6/7 of *Arabidopsis* flower development, the *DR5::GFP* reporter shows a diffuse distribution in the gynoecium primordium followed by accumulation of auxin at two lateral foci at the apex (stages defined in [5,16]) (Figure 2). This appears to be facilitated by the auxin efflux carrier, PIN1, as *PIN1::PIN1-GFP* expression shows PIN1 polarity converging at these sites prior to the formation of the foci. These foci possibly act as sinks that drive apical PIN1 polarity in the epidermal layers [14,8]. The establishment of these two lateral foci and the transport of auxin towards them are required for proper apical-basal patterning and growth [8]. Such a flux of auxin towards a distal maximum is a general

Figure 1



*Arabidopsis thaliana* gynoecium. The different morphological axes of the gynoecium are shown. The left panel shows a gynoecium cross section, while the right shows a scanning electron micrograph. Both are false-coloured to describe and distinguish the individual tissues (see colour code on the right). Scale bars, 100  $\mu$ m.

Figure 2



Distinct hormonal boundaries of auxin (red) and cytokinin (yellow) at different developmental stages of the *Arabidopsis* gynoecium with distribution of the hormones at stages 7 (left), 8/9 (middle) and 10–13 (right). Top views are given for stage 7 and 8/9, while cross sections at indicated positions are shown for stage 10–13.

mechanism in plant organ formation to guide growth [11,17]. From stage 8, the medial and lateral vascular bundles start to develop and PIN1 shows basal localization in the developing vasculature indicating a downward flux of auxin [14]. At stage 8/9, the bilateral symmetry of the developing, cylindrical gynoecium is broken and the

radially symmetrical style develops. This switch in symmetry is facilitated by the apolar localization of PIN1 and PIN3, and the appearance of two medial auxin foci which subsequently fuse with the lateral foci to form a DR5 ring at the gynoecium apex (Figure 2). The formation of this ring-formed auxin maximum is required for radial style

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