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Shattering fruits: variations on a dehiscent theme

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Fruits are seed dispersal units, and for that they have evolved different strategies to facilitate separation and dispersal of the progeny from the mother plant. A great proportion of fruits from different clades are dry and dehiscent, opening upon maturity to disperse the seeds. In the last two decades, intense research mainly in Arabidopsis has uncovered the basic network that controls the differentiation of the Arabidopsis fruit dehiscence zone. This review focuses on recent discoveries that have helped to complete the picture, as well as the insights from evo-devo and crop domestication studies that show how the conservation/variation of the elements of this network across species accounts for its evolutionary plasticity and the origin of evolutionary innovations.

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Introduction

Fruits are a major evolutionary innovation of angiosperms, which serve two main purposes: to protect the developing seeds and to facilitate offspring dispersal. This last function has great ecological importance and explains the high adaptive forces that have driven the huge diversity in morphology and function of fruits, which usually co-evolve with dispersal vectors [1]. The most abundant fruit types found are dry dehiscent, dry indehiscent and fleshy, and transitions between the different types are very frequent within clades, indicating their huge adaptive value and the likely plasticity of a common basic genetic ground that can easily accommodate changes to evolve new morphologies and dispersal strategies.

According to definition, a fruit is a seed dispersal unit, thus implying that a separation process is involved. To disperse the seeds, fruits can abscise from the plant themselves, or they can open (dehisce) and free the seeds, which have to separate from the mother tissues as well. These processes, fruit abscission, fruit dehiscence and seed abscission, have some common elements: a layer with small cells held together by the extracellular matrix formed at the breaking point, and lignification of cells at surrounding tissues. For separation to occur, physical forces have to trigger the detachment of cells at the separation layer, in an interplay that involves weakening of cell adhesion with tensions provided by the surrounding tissues or external agents. In fruit dehiscence (also known as pod shattering), these tensions usually come from pod walls, mediated by the differential mechanical properties of lignified and non-lignified tissues and changes in turgor associated to fruit maturation (Figure 1).

Fruit dehiscence and abscission have been extensively studied, both for their biological importance and as immediate targets for crop improvement. Here we review the last contributions to our understanding of dehiscence in dry fruits, and how comparative studies of natural variation or man-driven selection in crop domestication can help to complete a picture where still we can find important gaps.

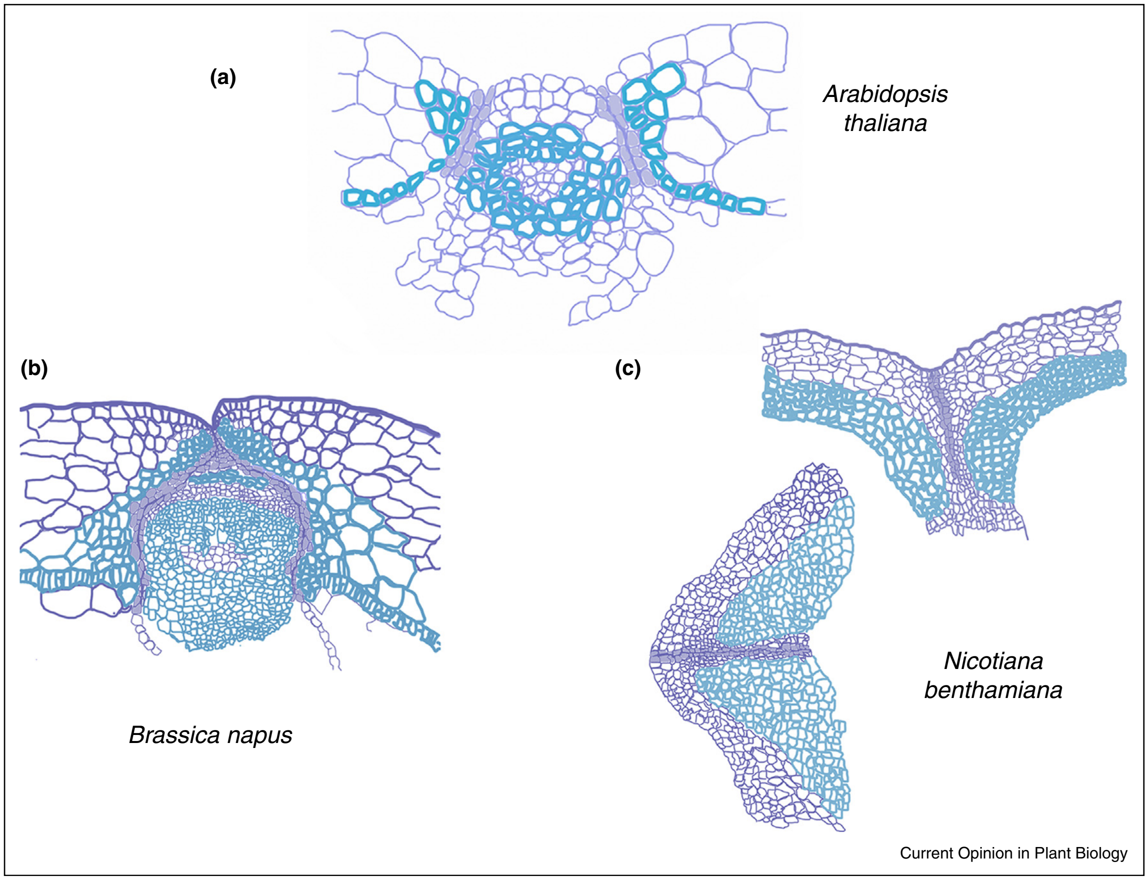
Genetic networks directing fruit dehiscence in Arabidopsis

The major players, the influencers, the newcomers and a few open questions

The basic components of the genetic network directing the morphogenesis of the dehiscence zone (DZ) in the Arabidopsis fruit have been known for several years. In brief, four transcription factors are expressed at the valve margin to direct DZ formation. SHATTERPROOF1 (SHP1) and SHP2 redundantly upregulate INDEHISCENT (IND) and ALCATRAZ (ALC) (Figure 2). In *shp1 shp2* and *ind* mutants, fruits lack lignified and separation layers and are fully indehiscent, while *alc* mutants show only defects in the separation layer, which no longer shows the typical small cells and the separation plane [2–4]. Two additional transcription factors, FRUITFULL (FUL) and REPLUMLESS (RPL), act in the valves and in the replum, respectively, to confine the expression of the DZ genes to the valve margin [3,5,6]. This relatively simple network and the regulatory interactions established among these components are largely sufficient to explain DZ formation, building the scaffold on which the basic blocks are defined.

More recently other players have been identified, which appear to modulate the size and position of the DZ or to contribute in partially redundant manner to the functions

Figure 1



Morphology of the dehiscence zone of fruits from different species. *Arabidopsis thaliana* **(a)**, *Brassica napus* **(b)** and *Nicotiana benthamiana* **(c)**, both at the valve margin (also known as septicidal, top) and at the middle of the pod wall (a.k.a. loculicidal, bottom). Lignified cells are depicted in light blue, and cells at the separation layer in grey. In all cases, despite different morphologies, cells at the separation layer are small and define a fracture plane, and are adjacent to lignified tissue.

of the FUL/SHP/IND/ALC/RPL factors, but are not essential to DZ formation. Among them, factors like BREVIPEDICELLUS (BP), NO TRANSMITTING TRACT (NTT) or WUSCHEL-RELATED HOMEOBOX 13 (WOX13) [7–9], generally associated to meristem-related functions, act in the replum and control replum width. Conversely, genes related to lateral organ development, like *FILAMENTOUS FLOWER*, *ASYMMETRIC LEAVES1* or *ASYMMETRIC LEAVES2*, act in the valves [7,10]. Interestingly, boundary genes, which in the shoot apex mark the division between meristematic and lateral domains, are also expressed in the valve margins and show similar regulatory interactions with the rest of the network [11], which might suggest their possible role in the determination of DZ position (Figure 2).

That meristem-related factors are expressed in the replum and the factors associated to organ differentiation are expressed in the valves has suggested that this network was coopted to establish medial (replum) versus lateral (valve) fate in the gynoecium [12–14]. It is likely that its major role would be the specification of the medial meristematic ridge that forms the placenta and ovules, as strongly supported by the characterization of the transcriptome of the medial domain in early stages of gynoecium development, which extensively overlaps with that of other meristems in the plant [15•]. However, they might be also working upstream the FUL/SHP/IND/ALC/RPL network to regulate their spatial distribution.

Recently, is has been uncovered that APETALA2 (AP2), best known because it controls perianth organ identity, negatively regulates both the DZ factors, *SHP* and *IND*, and the replum factors, *RPL* and *BP*, to ensure proper expression levels of all these genes and to restrict DZ and replum expansion to the valves [16]. Furthermore, FUL, together with ARF6 and ARF8, repress AP2 activity in the valves through activation of miR172 in this domain, thus uncovering the participation of posttranscriptional regulation in Arabidopsis fruit development (Figure 2). When AP2 activity is allowed in the valves, cell growth is