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MOSS DEVELOPMENT

Starting BELL for embryos

Major life cycle transitions happen after changes in stem cells trigger new developmental programs. In moss, expression of the homeobox transcription factor BELL1 is sufficient to induce sporophyte stem cells from the gametophyte phase, without having to go through fertilization.

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Land plants go through diploid sporophyte and haploid gametophyte stages of variable relative importance, during which different developmental programs are implemented. This development is mostly initiated and managed by the meristems, small groups of cells located at the body tips, and the change in meristem characteristics mirrors the change of developmental programs. In a study published in this issue, Reski and colleagues[1] show that, in the moss *Physcomitrella patens*, the ectopic expression of the transcription factor PpBELL1 induces mostly complete sporophyte development from gametophyte tissue, leading to viable spores through meiosis.

In angiosperms, during the dominant diploid sporophyte stage, the vegetative shoot apical meristem continuously produces leaves, stems and other aerial organs while maintaining itself, and then switches to a reproductive program to form

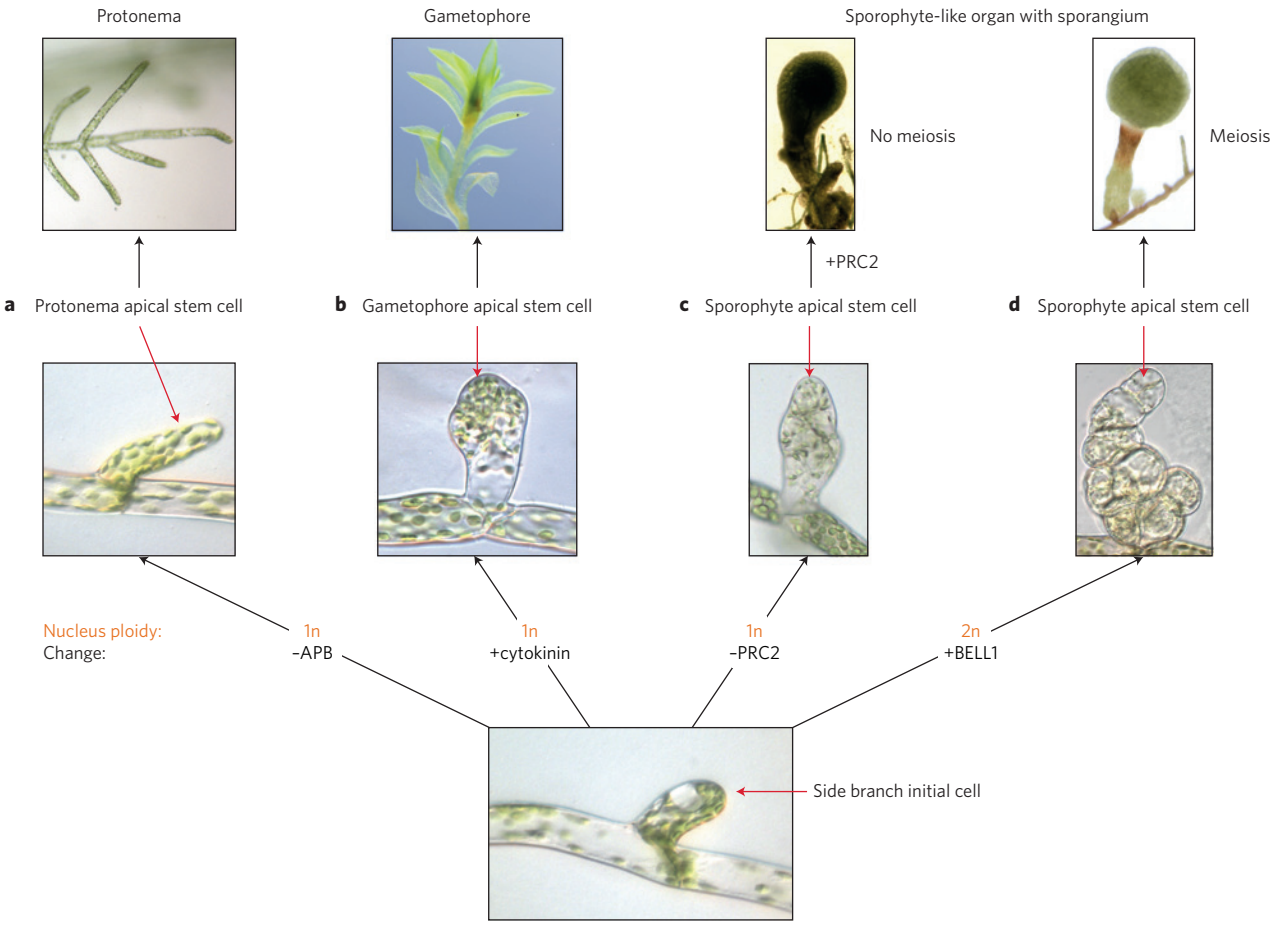

Figure 1 | BELL1, a molecular switch to modify stem cell potential. **a**,**b**, A side branch initial cell (bottom) initiated from a differentiated protonema cell becomes a protonema apical stem cell (**a**) or a gametophore apical stem cell (**b**) with the right combination of phytohormones and APB transcription factor[12] in the gametophyte. **c**, Deletion of a PRC2 component transforms a side branch initial cell into a sporophyte apical stem cell, and subsequent induction of the PRC2 gene results in a sporangium-like organ but without meiosis. **d**, Overexpression of the *PpBELL1* gene in endoreduplicated protonemata transforms a diploid side branch initial cell into a sporophyte apical stem cell that forms a sporophyte-like body topped by a sporangium in which meiosis occurs. This development stage is quite similar to the wild-type sporophyte. Images in **d** reproduced from ref. 1, Nature Publishing Group; all other images reproduced with permission from ref. 12, © 2012 Development.

flowers. Quite differently, the gametophyte bodies are composed of several cells and do not have meristems, and cannot survive very long without the physical and trophic support of the sporophyte body. Meristems contain multiple stem cells, which have the ability to self-renew and produce differentiated cells. In flowering plants, it is not clear whether the change in meristem features is a cause or a consequence of the change in stem cell state.

Bryophytes such as mosses and liverworts form a monophyletic group of non-vascular plants from the basal extant lineage of land plants[2]. Their meristem is composed of a single stem cell located at the body extremities, and the status of this cell can lead to different types of meristems and developmental programs. *P. patens* produces only one type of stem cell during the short diploid sporophyte stage: the first zygotic cell division forms one sporophyte apical stem cell, which gives birth to almost all the cells composing the sporophyte. At the start of the dominant and much longer haploid gametophyte phase, the first cell division of a spore produces a protonema apical stem cell that can create up to seven types of stem cell[3]. Therefore, the life cycle of bryophytes can be viewed as periodic modifications of stem cell properties, themselves partially dependent on the ploidy phase. Meiosis and fertilization are the 'tick marks' of the bryophyte's life cycle.

In *P. patens*, protonemata are filamentous bodies growing apically in the early gametophyte. Under the influence of hormones and nutritional factors, they can produce, from a differentiated subapical cell, a side bud with multipotent stem cell ability (Fig. 1). This side branch initial cell has the potential to develop into another protonema, or a shoot-like body bearing sperm and eggs called a gametophore. Auxin, cytokinin and their downstream genes regulate the fate of this initial cell[3]. Targeted deletions of the genes *CURLY LEAF* (*CLF*) or *FERTILIZATION-INDEPENDENT ENDOSPERM* (*FIE*) — both encoding interacting components of the polycomb repression complex 2 (PRC2) involved in histone H3K27 trimethylation and chromatin remodelling — cause the side branch initial cell to become a stem cell that is still haploid but sporophyte-like[4,5]. During regular development, sporophyte stem cells divide mitotically approximately 10 times, and then the produced diploid sporophyte body starts to form sporangium in which spores are produced by meiosis. As PRC2 is necessary for sporangium formation as well as for the repression of the cell fate change from a side branch initial cell to a sporophyte stem cell in the gametophyte, the deletion mutant does not form sporangium. Ectopic induction of CLF leads to a sporangium-like organ but meiosis is not observed, probably because of the haploid nature.

The three-amino-acid-loop-extension (TALE) class of homeodomain proteins contains KNOX and BELL subclasses, which function as heterodimers in regulating shoot meristem organization and other sporophyte development processes in angiosperms[6]. The divergence of the two subclasses predates the origin of land plants[7]. In the unicellular chlorophyte *Chlamydomonas reinhardtii*, KNOX and BELL proteins are separately expressed in each gamete of different sex, and fertilization results in the formation of heterodimers that then move to the nucleus to regulate zygote genes[8]. Even though these KNOX and BELL heterodimers are sufficient to trigger the diploid phase in unicellular green algae, it is not a plausible scenario in land plants, because loss-of-function *KNOX* mutants are still able to form zygotes and produce sporophyte stem cells[9,10].

However, Reski and colleagues[1] now report that ectopic overexpression of the *Arabidopsis thaliana BELL1* orthologue *PpBELL1* results in sporophyte apical stem cells budding from endoreduplicated protonemata cells, although haploid side branch initial cells are not changed. The developmental program proceeds further, as the induced diploid sporangia form spore tetrads that are probably produced by meiosis, although spores are not fully mature and less viable than wild type. On the other hand, zygotes of *PpBELL1* deletion mutants do not divide to form a sporophyte apical stem cell. These results suggest that *PpBELL1* is both necessary and sufficient to trigger sporophyte apical stem cell formation from gametophyte tissue. However, the relationship between PRC2 and BELL1 is a remaining open question because of the discrepancy between their expression patterns: although *PpBELL1* is repressed by PRC2 in protonemata, both the PRC2 genes *CLF* and *FIE* are co-expressed with *BELL1* in egg cells and during sporangium development.

The charophyte green algae from the Zygnematophyceae class (a sister group closely related to extant land plants) do not form a multicellular sporophyte body and a zygotic cell that proceeds to meiosis. Therefore, the evolutionary innovation of mitotic divisions after zygote formation by the sporophyte apical stem cell was suggested to be a critical change[11]. The finding of PpBELL1 involvement in this process in the basal land plant lineage is a new clue to understanding the molecular events that facilitated their colonization of Earth continents. ❐

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