Title

Abscisic acid switches cell division modes of asymmetric cell division and symmetric cell division in stem cells of protonemal filaments in the moss *Physcomitrium patens*

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Running title

Cell division modes switched by ABA in moss

Abbreviations

ABA, abscisic acid; ACD, asymmetric cell division; SCD, symmetric cell division

Figures: 4

Abstract

Multicellular organisms regulate cell numbers and cell fate by using asymmetric cell division (ACD) and symmetric cell division (SCD) during their development and to adapt to unfavorable environmental conditions. A stem cell self-renews and generates differentiated cells. In plants, various types of cells are produced by ACD or SCD; however, the molecular mechanisms of ACD or SCD and the cell division mode switch are largely unknown. The moss *Physcomitrium* (*Physcomitrella*) *patens* is a suitable model to study plant stem cells due to its simple anatomy. Here, we report the cell division mode switch induced by abscisic acid (ABA) in *P. patens*. ABA is synthesized in response to abiotic stresses and induces round-shape cells, called brood cells, from cylindrical protonemal cells. Although two daughter cells with distinct sizes were produced by ACD in a protonemal stem cell on ABA-free media, the sizes of two daughter cells became similar with ABA treatment. Actin microfilaments were spatially localized on the apices of apical stem cells in protonemata on ABA-free media, but the polar accumulation was lost under the condition of ABA treatment. Moreover, ABA treatment conferred an identical cell fate to the daughter cells in terms of cell division activity. Collectively, the results indicate ABA may suppress the ACD characteristics but evoke SCD in cells. We also noticed that ABA-induced brood cells not only self-renewed but regenerated protonemal cells when ABA was removed from the media, suggesting that brood cells are novel stem cells that are induced by environmental signals in *P. patens*.

Key words

51 Abscisic acid, Asymmetric cell division (ACD), *Physcomitrium patens*, Stem cell,

52 Symmetric cell division (SCD)

Text

Stem cells in multicellular organisms continuously produce various types of cells with diverse functions throughout their life cycle. Stem cells are relatively undifferentiated cells that have the characteristics of generation of differentiated cells and self-renewal for maintaining stem cell identity, and these characteristics are essential for the maintenance of a continuous cell population (Morrison and Kimble 2006). Asymmetric cell division (ACD) in stem cells generates two daughter cells with distinct fates of stemness and differentiation, while symmetric cell division (SCD) produces two daughter cells with equivalent or similar shapes, sizes or fates (Tajbakhsh et al. 2009). During ACD, stem cells establish an intracellular asymmetry of organelles and cellular structures including cytoskeletons. The asymmetric inheritance of cell context generates the distinct cell fates of two daughter cells (Sunchu and Cabernard 2020). In plants, activity of the meristem, which is composed of various types of stem cells, is regulated by developmental and environmental signals (Harris 2015; Pillitteri et al. 2016; Wybouw and Rybel 2019). Whereas the molecular mechanism of ACD in a certain stem cell, e.g., cortical-epidermal initials in root apical meristem, has been well studied (Fisher and Sozzani 2016), information on ACD or SCD in the other plant stem cells is limited. During embryogenesis or guard cell formation, ACD and SCD also play pivotal roles in specialized cell production (Petricka et al. 2009). However, we still need to learn much more; for example, how cell division modes are switched during development and how such a division mode is spatio-temporally regulated in response to differential environmental conditions.

Abscisic acid (ABA) is synthesized in plant cells in response to abiotic stresses and is a well-known phytohormone that regulates various abiotic stresses, seed dormancy and

77 germination, and stomatal closure (Harris 2015; Munemasa et al. 2015; Shu et al. 2016).
78 The response to ABA is initiated, after perception, by activation of a signaling consisting
79 of kinase cascades to activate the downstream transcription pathway. Recent studies have
80 revealed conservation of the core components of ABA signaling from bryophytes to
81 angiosperms (Komatsu et al. 2020). The moss *Physcomitrium patens* is used for evo-devo
82 study in land plants (Naramoto et al. 2021), and it consists of at least eight stem cells in
83 its life and possesses exposed stem cells on the edge of filamentous protonemata (Kofuji
84 and Hasebe 2014). In the presence of ABA, the protonemal cells from a variety of mosses
85 exhibit cell-morphological changes from cylindrical shape to more spherical, thick-
86 walled cells with segmented vacuoles, which are called brood cells (also called
87 brachycytes, brood bodies or diaspores) (Goode et al. 1993; Mallon et al. 2006; Martinez
88 et al. 2011; Schnepf and Reinhard 1997; Nagao et al. 2005), and indeed, some mosses use
89 brood cells as a dispersal unit for propagation (Glime and Bisang et al. 2017). Brood cell
90 formation is, at least partly, governed by the ABA signaling that is conserved among land
91 plants (Komatsu et al. 2013; Mengkai et al. 2018; Saruhashi et al. 2015; Shinozawa et al.
92 2019; Stevenson et al. 2016), and brood cells are tolerant to various abiotic stresses such
93 as desiccation and freezing stresses (Minami et al. 2003; Stevenson et al. 2016). In the
94 current study, we examined cell sizes, cytoskeleton and cell fate regulation during brood
95 cell formation, and we found that pivotal features of ACD were suppressed by ABA.
96 Hence, we propose a novel system to study switching between ACD and SCD of stem
97 cells through ABA signaling.
98 *P. patens* (Hedw.) Bruch & Schimp subsp. Patens Tan strain was used as the wild type
99 (Nishiyama et al. 2000). *P. patens* was cultured on cellophane mounting on BCDAT or
100 BCDATG solid media with 0.8% (w/v) agar (Nacalai Tesque) and 1% (w/v) glucose

(FUJIFILM Wako Pure Chemical) at 25°C under continuous white light (40-50 μmol m^{-2} s^{-1}) (Nishiyama et al. 2000). To compare sizes of daughter cells, the ratio of the section area of an apical cell or a side branch initial to a basal daughter cell, which were originated from the same mother cell, was calculated. Protonemata were transferred onto BCDATG media containing 50 μM ABA, referring to ABA concentration in the previous research (Nagao et al. 2005). Section areas of an apical cell, a side branch initial and a basal cell were measured using Image J software (https://imagej.nih.gov/ij/). To examine the cytoskeleton distribution in an apical stem cell in the protonema, localization of the actin marker LifeAct-Venus (Era et al. 2009) was observed. Transgenic protonemata carrying LifeAct-Venus were transferred onto BCDAT solid media containing 50 μM ABA. The fluorescence in chloronemal cells was observed with an inverted microscope (ECLIPSE Ti-E, Nikon) equipped with a mercury fluorescence source (C-SHG1, Nikon) at 0, 3 and 5 h after transferring. To examine cell division activities of protonemata with ABA treatment, cell division of daughter cells was examined. Protonemata were transferred onto BCDATG solid media containing 50 μM ABA and daughter cells, which were produced by the cell division of a basal daughter cell, were observed at 0, 25 and 96 h after transferring. The ability to regenerate chloronemal cells from brood cells was examined. The brood cells, which were induced by 50 μM ABA treatment for 10 d, were transferred onto ABA-free media and then chloronemal regeneration from the brood cells was observed at 0 and 24 h after transferring.

Apical stem cells of protonemata produce daughter cells with distinct sizes and nature by ACD under normal conditions (Kofuji and Hasebe 2014; Figure. 1A). A side branch initial is also produced as a stem cell from a protonemal cell by the mode of ACD (Kofuji and Hasebe 2014; Figure. 1A). In contrast, ABA-treated protonemal cells display

transverse division formed almost in the middle of the mother, protonemal cells (Schnepf and Reinhard 1997), and the cell division induced by ABA seems to have similar features to those of SCD; that is, cell sizes and cell fates of two daughter cells are equal or very similar. To verify this, we first compared the sizes of two daughter cells, which were produced within 2 h since cell division of the mother cell occurred. While the ratio of section areas of the apical cells (A) to basal cells (B) was 1: 1.63 on ABA-free solid media (Figure 1B, Mock, Apical), on media containing 50 μM ABA, the ratio became 1: 1.10 (Figure 1B, 50 μM ABA, Apical). Moreover, in the basal parts of protonemata, while the ratio of the side branch initials (A) to basal cells (B) was 1: 4.21 on ABA-free media (Figure 1 B), the ratio of the two daughter cells was 1: 1.53 on media containing 50 μM ABA. These results suggest that ABA-induced cell division lost the characteristic of ACD; that is, two daughter cells having similar sizes were produced in protonemata, which is a feature of SCD. Another characteristic of ACD is the establishment or maintenance of intracellular asymmetry. In fact, apical stem cells of protonemata are highly polarized cells that exhibit tip growth under normal culture conditions (Rounds and Bezanilla 2013). When we observed the actin marker LifeAct-Venus, actin cytoskeleton was highly accumulated on the apex of apical stem cells on ABA-free media (Figure 2 Mock). In contrast, the polarized accumulation was lost within 3 h after 50 μM ABA treatment (Figure 2 50 μM ABA), suggesting that intracellular asymmetry is attenuated by ABA.

ACD also has the characteristic of producing two daughter cells that have distinct cell fates. A protonemal apical stem cell divides asymmetrically to produce two daughter cells, and the apical daughter cell behaves as a stem cell that can continuously divide to produce more daughter cells (Figure. 1A ACD of apical stem cell). On the other hand, the basal

149 daughter cell shows greatly reduced cell division activity and it usually divides only once
150 again or twice at most when it produces side branch initial cells (Figure. 1A Side branch
151 initial formation), suggesting that the two daughter cells produced by ACD of an apical
152 stem cell have distinct cell proliferation potentials. To examine whether two daughter
153 cells produced by ABA treatment have similar cell proliferation potentials or not, we grew
154 protonemata on media containing 50 μM ABA. As shown in Figure. 3, at 96 h after
155 transferring onto media containing 50 μM ABA, the basal side of the daughter cell, now
156 converting to a brood cell, was able to produce daughter cells continuously as well as the
157 apical side of the daughter cell, suggesting maintenance of cell proliferation ability even
158 in basal daughter cells. Thus, ABA-induced brood cells loose prominent characteristics
159 found in ACD but exhibit several SCD features and, consequently, both daughter cells
160 have the ability to self-renew.

161 Stem cells are cells that have the potential to self-renew and can differentiate into
162 different types of cells. We next examined whether brood cells have the ability to generate
163 a different type of cell. To this end, brood cells were induced by 50 μM ABA for 10 d
164 and transferred onto ABA-free media. After 10 days of ABA treatment, we noticed that
165 the connection between the cells was weakened and the brood cells were easily loosened
166 into pieces as small clumps of cells (Figure. 4A, 0 h). Then at 24 h after transfer, some
167 brood cells showed protrusions, likely resuming tip growth, and others regenerated
168 chloronemal cells by ACD (Figure. 4A, 24 h), suggesting that brood cells maintain the
169 ability to generate a distinct type of cell. Collectively, the results indicate that brood cells
170 have characteristics of stem cells, which possess the abilities to self-renew and to generate
171 distinct cell types.

172 Although many studies have been performed to try to determine the regulatory

mechanism of stem cells in plant meristems in angiosperms, it is still difficult to track a single stem cell behavior and uncover the regulatory mechanism at a single cell level. *P. patens* possesses a single stem cell on each of the edges of protonemal filaments, a chloronema apical stem cell, a caulonema apical stem cell or a gametophore apical stem cell (Kofuji and Hasebe, 2014). Because these apical stem cells are exposed outside of the tissue, the single stem cells can be observed continuously with a microscope. In the present study, we found that different modes of cell division, ACD and SCD, are used in *P. patens* protonemal tissue depending on the growth environment (Figure. 4B). Under normal growth conditions, protonema apical stem cells continue to self-renew and to produce differentiated protonemal cells with distinct cell proliferative activity by ACD to expand their growth niche. On the other hand, under stress conditions, ABA induces stress-tolerant stem cells, brood cells, with the number of stress-tolerant cells being increased by SCD, thus increasing their own survival potential. When the stress conditions have disappeared, the brood cells differentiate into protonemal cells again by ACD and continue growing to expand their growth range. Hence, brood cells are novel stem cells that temporarily appear in response to environmental stress conditions.

How is the switching between ACD and SCD controlled? We speculate that ABA induces a mechanism that suppresses ACD under stress conditions. Rho of plants (ROPs), which are small GTPases, are essential for cell polarity establishment and maintenance, which are also important for asymmetric organization of the cytoskeletal distribution (Feiguelman et al. 2018). The activity of ROPs is positively regulated by ROP guanine nucleotide exchange factors (RopGEFs). In the absence of ABA, RopGEFs negatively regulate the downstream factors of the ABA signal transduction by directly interacting with type 2C protein phosphatases (PP2Cs), inhibitory phosphatases of ABA signaling

(Li and Liu 2012; Yu et al. 2012). On the other hand, in the presence of ABA, i.e., under abiotic stress conditions, ABA induces the degradation of RopGEFs to facilitate ABA signal transduction by releasing the interaction between PP2Cs and RopGEFs, suggesting the significance of the PP2C-RopGEF-ROP circuit loop to control critical cellular processes via ABA signal transduction during growth of *Arabidopsis thaliana* (Li et al. 2016). While PP2C-RopGEF interaction has not been shown in *P. patens*, considering that PP2C, RopGEFs and ROPs are evolutionarily conserved in *P. patens* (Ito et al. 2014; Komatsu et al. 2020), we postulate that the change in the cell division mode from ACD to SCD under stress conditions might be mediated through the degradation of RopGEFs induced by ABA in *P. patens*. In *A. thaliana*, stomatal lineage is initiated from meristemoid mother cells, which undergo ACD to generate meristemoids. ABA represses meristemoid formation (Tanaka et al. 2013), suggesting that ABA suppresses ACD of meristemoid mother cells. It is tempting to speculate that ABA switches cell division modes by suppressing cell polarity signaling and this mechanism might be conserved in land plants.

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Author contributions

AH performed experiments, wrote the manuscript and contributed to Figures 1, 2 and 4. KN performed experiments and contributed to Figures 1, 3, and 4. TF conceptualized the

study and supervised the writing of the manuscript.

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Figure legends

Figure 1. Ratios of section areas of apical stem cells or side branch initials to basal cells

(A) A schematic model of cell division patterns in protonemal cells on ABA-free media. Apical stem cells divide asymmetrically to produce daughter cells, an apical daughter cell and a basal daughter cell. While the apical daughter cell maintains cell division activity, the basal daughter cell, becoming a basal cell, shows reduced cell division activity and it divides up to two times to produce two more daughter cells. (B) Protonemata were transferred onto media containing 50 μM ABA. The section areas of apical cells (A), side branch initials (A) and basal cells (B), which were just produced by cell division of the mother cells, were measured and the ratios of the section areas (B/A) were calculated. Values are means ± SD of 11-20 independent protonemal filaments. Asterisks indicate significant difference between mock and ABA treatments (***P<0.001; Student's t-test). Scale bars =50 μm. Daughter cells with similar sizes were produced under the condition of ABA treatment.

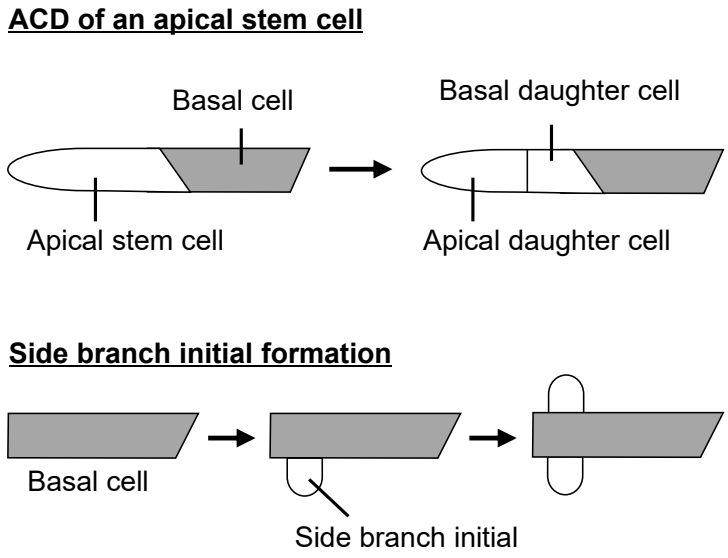
Figure 2. Distribution of an actin marker in apical stem cells of protonemata

Protonemata were transferred onto solid media containing 50 μM ABA. Fluorescence of the actin marker LifeAct-Venus in 3-8 independent chloronemal cells was observed with an inverted microscope at 0, 3 and 5 h after transferring. The same cells were not sequentially observed after transferring but representative images are shown at each time point. Arrowheads indicate accumulation of LifeAct-Venus at the apices of chloronemal cells. Scale bars = 50 μm. The polarized accumulation of LifeAct-Venus, which was

341 highly accumulated on the apices of apical stem cells on ABA-free media, was lost within
342 3 h after 50 μM ABA treatment.
343
344 **Figure 3. Cell division activity of basal daughter cells after ABA treatment**
345 Protonemata were transferred onto solid media containing 50 μM ABA and cell division
346 was observed at 0, 25 and 96 h. Red dots indicate cells that originated from the basal
347 daughter cell (at 25 and 96 h). Black arrowheads indicate septum of basal daughter cells.
348 Scale bars =50 μm. The basal daughter cell at 0 h (shown by an open red circle)
349 continuously divided to produce 3 daughter cells, indicating maintenance of cell division
350 activity in the basal daughter cells as well as in the apical daughter cells.
351
352 **Figure 4. Chloronemal regeneration from brood cells**
353 Brood cells, which were induced by 50 μM ABA treatment for 10 d, were transferred
354 onto ABA-free media. Chloronemal regeneration from the brood cells was observed at
355 24 h after transferring. Scale bars =50 μm. A schematic model of the cell division mode
356 switching induced by ABA. Protonemata undergo ACD under normal conditions but
357 undergo SCD under stress conditions.

Top

A



B

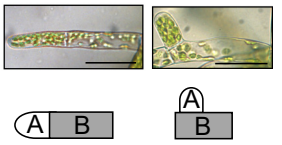
	Mock		50 μM ABA	
	Apical	Basal	Apical	Basal
				
Area ratio (A:B)	1:1.63 ± 0.3	1:4.21 ± 1.1	1:1.10 ± 0.3***	1:1.53 ± 1.3***

Figure number: Figure 1

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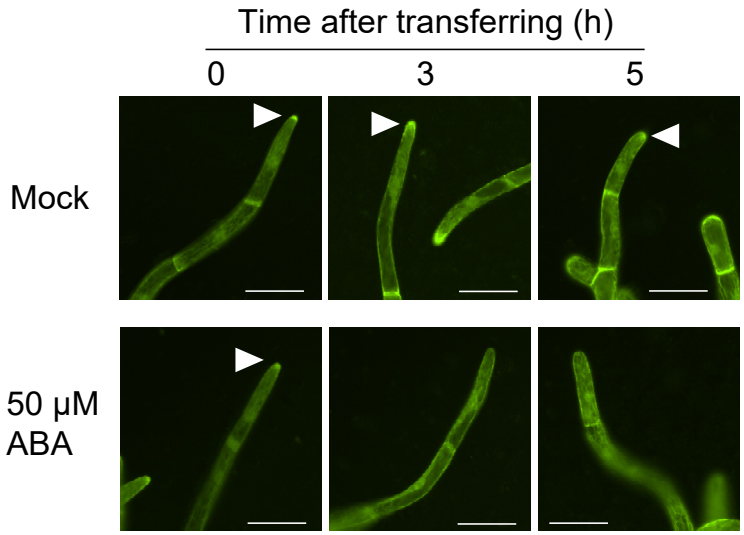
Tomomichi Fujita

Bottom

Top



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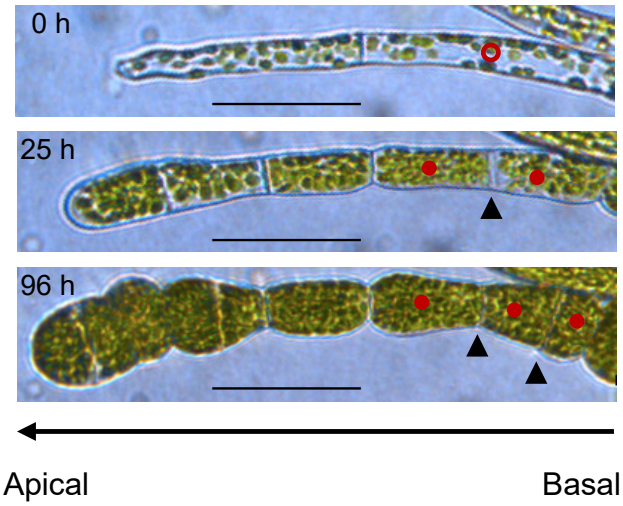

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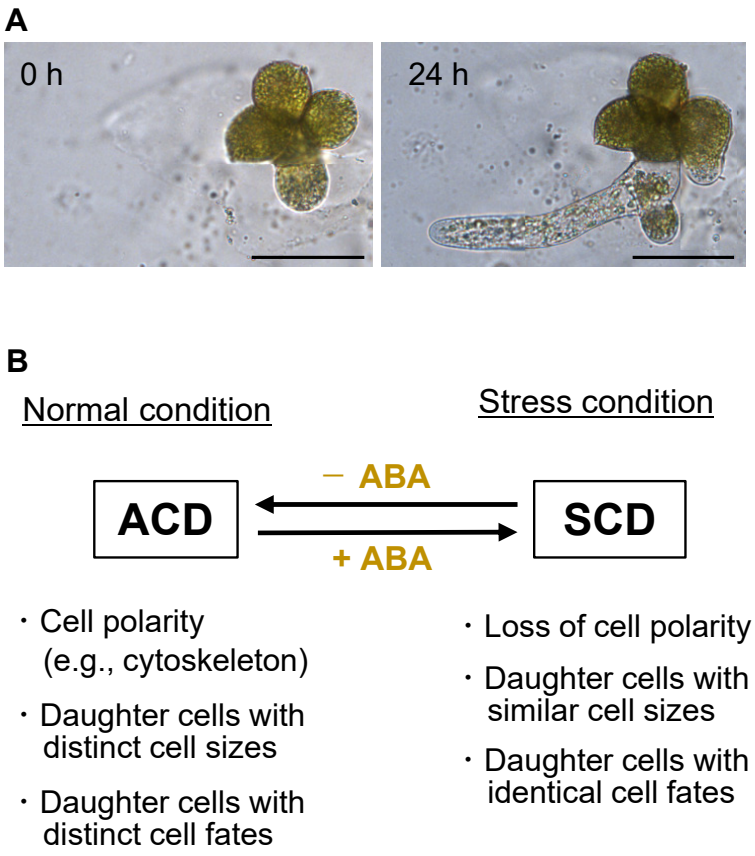

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