Opinion Article

Diploid Apogamy in Red Algal Species of the Genus *Pyropia*

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Bangiales is an order of red algae in the class Bangiophyceae of the division Rhodophyta [1,2] that has recently been subdivided into fifteen genera including *Bangia*, *Pyropia*, *Porphyra*, and *Boreophyllum* [3]. Most seaweeds in the Bangiales feature a heteromorphic haploid-diploid life cycle wherein both the haploid gametophyte and the diploid sporophyte develop multicellular bodies that appear in temporally distinct periods of the year [4-6]. In most plants and seaweeds, transitions from gametophyte to sporophyte and from sporophyte to gametophyte are triggered by fertilization of male and female gametes and meiosis, respectively [4-8]. However, meiosis is not involved in the formation of gametophytes in Bangiales, even though the transition from gametophyte to sporophyte is mediated by fertilization [9,10]. In the Bangiales, meiotic cell division instead occurs early during the development of gametophytes [11-20].

The life cycle of the marine red alga *Pyropia yezoensis*, in particular, thus does not conform to the general concept of a requirement for meiosis in gametophyte production. In fact, we recently demonstrated that gametophyte identity in *P. yezoensis* is established without meiosis in the conchosporangia, which are parasitically produced on sporophytes [10,21]. Based on these findings, we proposed that *P. yezoensis* has a triphasic life cycle consisting of gametophyte, sporophyte, and conchosporophyte, which represents novel nomenclature denoting the conchosporangium as a life cycle generation [21].

The production of diploid gametophytes without meiosis, as found in conchosporophytes of *P. yezoensis* [21], is generally designated as apospory, whereas the production of haploid sporophytes from somatic cells in haploid gametophytes without fertilization of gametes is named apogamy [8,21]. Apospory and apogamy together are termed apomixis and represent an asexual strategy

for reproduction from somatic cells without ploidy change [8,23], a phenomenon that has been observed primarily in ferns and vascular plants [22,24-26].

In seaweeds, production of sporophytes from somatic cells has been observed in thalli of *P. yezoensis* treated with hydrogen peroxide [10] and laboratory-cultured female gametophytes of *P. haitanensis* [27]. Although these phenomena were initially described as apogamy or parthenogenesis [10,27], these definitions may be misnomers. In the case of *P. yezoensis*, although the production of sporophytes from somatic cells fits apogamy, the resultant sporophytes were proposed to be diploid, whereas apogamous sporophytes should be haploid (Figure 1). The diploidy of the sporophytes produced from somatic cells was confirmed in *P. haitanensis* by karyotype analysis, which indicated that the ploidy of red-colored cells pre-programmed to generate sporophytes is autonomously doubled before the production of sporophyte filaments [27]. However, it is incorrect to describe this process as parthenogenesis, since parthenogenesis denotes the development of sporophytes from gametes (Figure 1). Therefore, neither apogamy nor parthenogenesis fully describes the aforementioned, unique phenomena in these two species of *Pyropia*. As far as we know, there is currently no nomenclature that denotes haploid somatic cell-derived generation of diploid sporophytes without fertilization.

In animals, fertilization-independent production of diploid zygotes through gamete duplication (chromosome duplication) is one of the strategies categorized as automixis (Figure 1), which refers to diploid parthenogenesis based on development of maternal oocytes and polar bodies produced by meiosis [28-30]. Since such a spontaneous chromosomal duplication is also observed in *P. haitanensis* [27], the production of sporophytes from somatic cells in *Pyropia* is partly analogous to gamete duplication in automixis. Given

that homologous recombination occurs during gamete duplication, automixis is recognized as a form of sexual reproduction [31].

Taking all of these cases together, it seems that sporophyte production from somatic cells in *Pyropia* can be viewed as a hybrid process similar to apogamy in plants and gamete duplication in animals, wherein the former establishes sporophyte identity in haploid gametophytic cells and the latter is responsible for the production of normal diploid sporophyte filaments. This should clearly be categorized as a form of apomixis, since the phenomenon is independent of fertilization. Thus, as shown in Figure 1, we tentatively designate this unique strategy “diploid apogamy” to distinguish it from the general term “apogamy,” which could be more specifically termed “haploid apogamy” because of the absence of ploidy change. This nomenclature is analogous to that used for parthenogenesis, which is subdivided into haploid parthenogenesis and diploid parthenogenesis in animals (Figure 1) [32-34]. In fact, spontaneous chromosome duplication was also observed in one-third of parthenosporophytes during the first cell division of non-fertilized gametes in the brown alga *Ectocarpus siliculosus* [35], indicating the presence of both haploid and diploid parthenogenesis in seaweeds. Thus, to distinguish between apogamous phenomena with and without chromosome duplication, it is reasonable to use the terms haploid and diploid apogamy.

As mentioned above, *P. yezoensis* and *P. haitanensis* utilize characteristic reproductive strategies such as apospory for the establishment of gametophyte identity and diploid apogamy for the production of normal diploid

sporophytes from haploid gametophytic somatic cells, respectively [10,27]. These findings suggest that there are unique regulatory mechanisms for reproduction in the genus *Pyropia*. Thus, further study on apomixis in *Pyropia* could provide new information about regulatory factors and genes involved in diploid apogamy and generation switches during the life cycle. By analogy, *E. siliculosus* life cycle mutants like *OUROBOROS* and *SAMSARA* have helped to elucidate the regulatory system of life cycle phase transitions [36,37]. However, no life cycle mutant has been reported in *Pyropia*, *Bangia*, and *Porphyra*. Therefore, future work should focus on isolating life cycle mutants to advance research on the regulatory mechanisms common to haploid-diploid life cycles, diploid apogamy, and apospory in the Bangiales.

References

- Garbary DJ, Hansen GI, Scagel RF (1980) A revised classification of the Bangiophyceae (Rhodophyta). Nova Hedw 33:145-166.
- Yoon HS, Müller KM, Sheath RG, Ott FD, Bhattacharya D (2006) Defining the major lineages of red algae (Rhodophyta). J Phycol 42: 482-492.
- Sutherland JE, Lindstrom SC, Nelson WA, Brodie J, Lynch MD et al. (2011) A new look at an ancient order: Generic revision of the Bangiales (Rhodophyta). J Phycol 47: 1131-51.
- Coelho SM, Peters AF, Charrier B, Roze D, Destombe C et al. (2007) Complex life cycles of multicellular eukaryotes: New approaches based on the use of model organisms. Gene 406:152-170.
- Cock JM, Godfroy O, Macaisne N, Peters AF, Coelho SM (2014) Evolution and regulation of complex life cycles: a brown algal perspective. Curr Opin Plant Biol 17: 1-6.
- Liu X, Bogaert K, Engelen AH, Leliaert F, Roleda MY et al. (2017) Seaweed reproductive biology: Environmental and genetic controls. Bot Mar 60: 89-108.
- Friedman WE (2013) One genome, two ontogenies. Science 339: 1045-1046.

8. Bowman JL, Sakakibara K, Furumizu C, Dierschke T (2016) Evolution in the cycles of life. *Annu Rev Genet* 50: 133-154.
9. Mikami K, Li L, Takahashi M. (2012) Monospore-based asexual life cycle in *Porphyra yezoensis*. In: Mikami K (ed). *Porphyra yezoensis*: Frontiers in Physiological and Molecular Biological Research. Nova Science Publishers, New York, USA. Pg no: 15-37.
10. Takahashi M and Mikami K (2017) Oxidative Stress Promotes Asexual Reproduction and Apogamy in the Red Seaweed *Pyropia yezoensis*. *Front Plant Sci* 8: 62.
11. Ma JH, Miura A (1984) Observations of the nuclear division in the conchospores and their germings in *Porphyra yezoensis* Ueda. *Jpn J Phycol* 32: 373-378.
12. Ohme M, Kunifuji Y, Miura A (1986) Cross experiments of the color mutants in *Porphyra yezoensis* Ueda. *Jpn J Phycol* 34: 101-106.
13. Burzycki GM, Waaland JR (1987) On the position of meiosis in the life history of *Porphyra torta*. *Bot Mar* 30: 5-10.
14. Ohme M, Miura A (1988) Tetrad analysis in conchospore germings of *Porphyra yezoensis* (Rhodophyta, Bangiales). *Plant Sci* 57: 135-140.
15. Tseng CK, Sun A (1989) Studies on the alternation of the nuclear phases and chromosome numbers in the life history of some species of *Porphyra* from China. *Bot Mar* 32: 1-8.
16. Mitman GG, van der Meer JP (1994) Meiosis, blade development, and sex determination in *Porphyra purpurea* (Rhodophyta). *J Phycol* 30: 147-159.
17. Yan XH, Li L, Aruga Y (2005) Genetic analysis of the position of meiosis in *Porphyra haitanensis* Chang et Zheng (Bangiales, Rhodophyta). *J Appl Phycol* 17: 467-473.
18. Wang J, Dai J, Zhang Y (2006) Nuclear division of the vegetative cells, conchosporangial cells and conchospores of *Porphyra yezoensis* (Bangiales, Rhodophyta). *Phycol Res* 54: 201-207.
19. Shimizu A, Morishima K, Kobayashi M, Kunitomo M, Nakayama I (2007) Identification of *Porphyra yezoensis* (Rhodophyta) meiosis by DNA quantification using confocal laser scanning microscopy. *J Appl Phycol* 20: 83-88.
20. Yan XH, Huang M (2010) Identification of *Porphyra haitanensis* (Bangiales, Rhodophyta) meiosis by Simple Sequence Repeat markers. *J Phycol* 46: 982-986.
21. Mikami K, Li C, Irie R, Hama Y (2019) A unique life cycle transition in the red seaweed *Pyropia yezoensis* depends on apospory. *Commun Biol* 2:229.
22. Sajeev S, Melo JS, Hegde S (2018) Gamma radiation-induced in vitro hormetic apogamy in the fern *Pityrogramma calomelanos* (L.) link. *Biosystems* 173: 221-224.
23. Chandra K, Pandey A (2017) Apomixis: a boon to plant breeding. *Int J Curr Microbiol App Sci* 6: 2619-2626.
24. Koltunow AM, Grossniklaus U (2003) Apomixis: A developmental perspective. *Annu Rev Plant Biol* 54: 547-574.
25. Grusz AL (2016) A current perspective on apomixis in ferns. *J Syst Evol* 54: 656-665.
26. Fei X, Shi J, Liu Y, Niu J, Wei A (2019) The steps from sexual reproduction to apomixis. *Planta* 249: 1715-1730.
27. Zhong C, Aruga Y, Yan X (2019) Morphogenesis and spontaneous chromosome doubling during the parthenogenetic development of haploid female gametophytes in *Pyropia haitanensis* (Bangiales, Rhodophyta). *J Appl Phycol* 1-13.
28. Rabeling C, Kronauer DJ (2013) Thelytokous parthenogenesis in eusocial Hymenoptera. *Annu Rev Entomol* 58: 273-292.
29. Taylor EN, Booth W (2016) Rattlesnakes as models for reproductive studies of vertebrates. In: Schuett GW, Feldner MJ, Smith CF, Reiserer RS (eds.). *Rattlesnakes of Arizona*, vol. 2 Conservation, Behavior, Venom, and Evolution, ECO Wear & Publishing, Rodeo, New Mexico, USA. Pg no: 123-157.
30. Engelstädter J (2017) Asexual but not clonal: Evolutionary processes in automictic populations. *Genetics* 206: 993-1009.
31. Mogie M (1986) Automixis: its distribution and status. *Biol J Linnean Soc* 28: 321-329.
32. Pinyopummin A, Takahashi Y, Hishinuma M, Kanagawa H (1994) *In vitro* development of mouse parthenogenetic embryos to blastocysts: Effect of embryo dens. *J Reprod Dev* 40: 55-58.
33. Sembon S, Fuchimoto D, Iwamoto M, Suzuki S, Onishi A (2011) Ploidy assessment of porcine haploid and diploid parthenogenetic embryos by fluorescent *in situ* hybridization detecting a chromosome 1-specific sequence, *Sus scrofa* Mc1 satellite DNA. *J Reprod Dev* 57: 307-311.
34. Vichera G, Olivera R, Salamone D (2013) Oocyte genome cloning used in biparental bovine embryoreconstruction. *Zygote* 21: 21-29.
35. Bothwell JH, Marie D, Peters AF, Cock JM, Coelho SM (2010) Role of endoreduplication and apomeiosis during parthenogenetic reproduction in the model brown alga *Ectocarpus*. *New Phytol* 188: 111-121.
36. Coelho SM, Godfroy O, Arun A, Le Corguillé G, Peters AF et al. (2011) *OUROBOROS* is a master regulator of the gametophyte to sporophyte life cycle transition in the brown alga *Ectocarpus*. *Proc Natl Acad Sci USA* 108: 11518-11523.
37. Arun A, Coelho SM, Peters AF, Bourdareau S, Pérès L et al. (2019) Convergent recruitment of TALE homeodomain life cycle regulators to direct sporophyte development in land plants and brown algae. *eLife* 8. pii: e43101.

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