Reproductive structures of Bostrychia simpliciuscula (Ceramiales, Rhodophyceae) in the field and in culture

Mitsunobu Kamiya*, John A. West** and Yoshiaki Hara*

*Institute of Biological Sciences, University of Tsukuba, Tsukuba, Ibaraki 305 JAPAN ** School of Botany, University of Melbourne, Parkville, Victoria 3052, AUSTRALIA

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Reproductive structures of Bostrychia simpliciuscula are described based on the field and cultured plants in Japan, Singapore and Australia. The reproductive organs of male and female gametophytes and carposporophytes are described for the first time. This species is usually unisexual and has a Polysiphonia-type life history pattern, however, a few bisexual plants developed from the tetraspore germlings of an isolate from Singapore. The carpogonial branch is mainly composed of 4 cells, rarely 3 cells, and this feature is common to many other Bostrychia species. The number and dividing pattern of cortical cells in spermatangial stichidia are more variable and complicated than those of other Bostrychia species.

Key Index Words: bisexual, Bostrychia simpliciuscula, Ceramiales, Polysiphonia-type life history, reproductive structure, Rhodomelaceae, Rhodophyceae

The genus *Bostrychia* is common to the mangroves and salt marshes of estuarine systems throughout the tropical and temperate regions of the world. B. simpliciuscula Harvey ex J. Agardh is known in Japan (Okamura 1907 as B. andoi, Tokida 1939, Kumano 1979 as B. tenuis f. simpliciuscula and B. hamanatokidai, Yoshizaki et al. 1983 as B. tenuis f. simpliciuscula), Australia (King & Puttock 1989), Hong Kong and Macao (Tseng 1943), Singapore (West 1991) and Fiji (South et al. 1994). This species is characteristically turfforming with the main axes 2-5 cm long, bearing lateral branches with 1-2 orders of additional branching that is partially or completely monosiphonous, peripherohaptera arising at branch nodes, with 4-6 pericentral cells each forming two vertical tier cells. In Japan, the species frequently grows associated with stem of reeds Phragmites communis Trin. or rocks in freshwater streams near estuaries and appears in higher zone than Caloglossa leprieurii f. continua (Okamura) Post and C. ogasawaraensis Okamura (Yoshizaki et al. 1983). The species is also growing with either the liverwort Lepidozia mamillaris Schiffner or the green alga Boodleopsis carolinensis Trono in turf at Singapore (West 1991).

The polyol content (D-sorbitol and D-dulcitol) of B. simpliciuscula laboratory cultured samples from Singapore was analyzed by Karsten et al. (1992) and is similar to that of most other Bostrychia species in which these compounds are required for osmoacclimation. D- sorbitol content (range 114-194, mean 161 μ mol g⁻¹ DW) was usually lower than D-dulcitol content (range 130-286, mean 216 μ mol g⁻¹ DW). The ecophysiology of one *B*. simpliciuscula isolate (no. 2963) from Singapore has been investigated by Karsten et al. $(1994).$

Yoshizaki et al. (1986, 1993) examined the phenology of B. simpliciuscula in the Kido River (Chiba Pref., Japan) but found no fertile gametophytes or tetrasporophytes. In field collections by various authors only a few tetrasporophytes bearing stichidia have been observed (Kumano 1979, King and Puttock 1989), and fertile gametophytes have never been recorded so far.

In this study, we could observe various reproductive states of this species in field and/or cultured plants. These field and laboratory investigations are not only considered appropriate to determine the overall life history of this species but also contribute the analysis of the taxonomic and phylogenetic relationships with other Bostrychia species.

Materials and Methods

The collection locality and date of Bostrychia simpliciuscula samples are listed in Table 1 with culture numbers for isolates established.

For Australian and Singapore isolates kept by West, collection, transport and culture procedures followed those of West and Calumpong (1988) except for the culture condition. The isolates cultured were maintained in Provasoli's enriched seawater (2 ml enrichment/l30 ppt sea water, see Starr and Zeikus 1993) at 10-20 μ mol photons m⁻²s⁻¹ cool white Huorescent lighting, 12: 12 LD, and 22-25°C. For some experiments to increase growth and tetrasporangial stichidial formation the irradiance was increased to 50 μ mol photons $m^{-2}s^{-1}$.

The Japanese isolates kept by Kamiya and Hara were put into 100 ml plastic cups containing 20-30 ml Provasoli's enriched seawater (20 ml enrichment/l 14 ppt sea water), and the isolates were maintained at 0.5- 9 μ mol photons m⁻²s⁻¹ cool white fluorescent lighting, $14:10$ LD, and $20-25$ °C. The medium were changed every one or two months. As needed in each culture for preventing diatom and cyanobacterium growth, 1 mg/l germanium dioxide and 30 mg/l streptomycin were added to the medium.

Both field and cultured specimens were stained for observing under light microscope by 0.04% cotton blue in seawater with 0.3% 1 N HC1, 10% formalin, 20% glycerol and 20% ethanol. Stained specimens were then mounted in 80% Karo Φ syrup in distilled water with 10% formalin.

For measuring the size of reproductive organs, 5-20 cultured plants from different localities were employed.

Results

Reproduction of field specimens. About fifty field specimens collected from each locality were surveyed for reproductive structures (Table 1). The tetrasporophytes with tetrasporangial stichidia were collected in only five localities, Aki River (2 plants), Mandai (1 plant), Nagara R. (18 plants), Shiira R. (12 plants) and Yorimo R. (3 plants), whereas no fertile gametophytes were found in field except one male gametophyte in Lim Chu Kang (Table 1).

Tetraspore germination. Almost all of the field plants used for culture experiments initially lacked reproductive organs. One month or more after the plants were inoculated into vessels containing PES media, they developed tetrasporangial stichidia. Freshly released tetraspores were 39-46 μ m diam. (mean 42 μ m, n = 10). As is characteristic of most Ceramiales, spore germination was bipolar with the first germ tube establishing the rhizoid filament and the second forming the erect axial shoot which then elongated rapidly forming a monosiphonous filament of 20 or more cells (1-2 mm long) before becoming polysiphonous (Fig. 1) and beginning the development of the first lateral branches (Fig. 2). The monosiphonous filament remained uniform in diameter (22-27 μ m) throughout development. The rhizoid pole development was repressed until the main shoot became polysiphonous and branched. Then the rhizoid began to elongate as a monosiphonous branch that was characteristically narrower and lighter in color than the erect axis (Fig. 2). New erect shoots arose as small bud-like initials from intercalary cells of the rhizoidal filaments (Fig. 2).

The plant was dichotomously or subdichotomously branched (Figs. $3, 4$), consisting of axial cells and pericentral cells, 100-180 μ m in diameter near the base. At the apex, a domeshaped apical cell cut off disc-shaped axial cells downward, and first pericentral cells were divided from the 4th-16th axial cell (Fig. 5). Each axial cell was surrounded by 4 pericentral cells near the apex and by 5

Table 1. Collection locality and date, culture number and reproductive state of B. simpliciuscula in the field and culture.

* " V " and \odot indicate vegetative plants bearing no reproductive organs and tetrasporophytes bearing tetrasporangial stichidia, respectively.

pericentral cells from the 10th-22nd segments downward. Each proximal pericentral cell divided directly from axial cells cut off a distal pericentral cell toward the apex (Fig. 6). In each segment, primary pit connections were seen between the axial cells and the proximal pericentral cells and also between the prox imal and distal pericentral cells (Fig. 6). The intersegmental secondary pit connections were always formed between the adjacent vertical pericentral cells (Fig. 6) except for the segments near the apex. Occasionally the second inter-/intra-segmental pit connections were seen between the adjacent vertical

pericentral cells. Lateral branches were partially, sometimes completely monosiphonous, and such monosiphonous branches reached 11-33 cells long (Fig. 4).

Peripherohaptera were slow to develop in culture, and the plants often reached 1-2 cm in length before peripherohaptera were formed. In field plants, peripherohaptera were less than 0.2 mm in length and often developed in tandem (Fig. 7), except for plants in Shiira River, which sometimes had long and sparse ones (max. 1 mm). Usually field plants had more pericentral cells elongating to form the peripherohapteral filaments than cul-

Figs. 1-6. Bostrychia simpliciuscula in culture.

Fig. 1. Three days old tetraspore germlings of no. 2963 isolate. Scale bar = 100 μ m.

Fig. 2. A twenty-five days old tetraspore germling of no. 2963 isolate. An erect main polysiphonous shoot (arrow) with first branches and basal system of branching rhizoids (arrowhead) are seen. Note a new erect shoot (double arrowhead) arising from the rhizoidal filament. Scale bar=300 μ m.

Fig. 3. A whole thallus of no. 2964 isolate. Scale bar = 3 mm .

Fig. 4. A part of branch in no. 755 isolate, showing partial monosiphonous branch. Scale bar = 100 μ m.

Fig. 5. Apex of an indeterminate branch, showing first pericentral cels divided from the 6th axial cel (arrow). Scale bar = 20μ m.

Fig. 6. A part of branch, showing that a proximal pericentral cell (ppc) divided from an axial cell (ax) cuts off a distal pericentral cell (dpc) toward the apex (left side). Note primary pit connections (arrow) and intersegmental secondary pit connections (arrowhead). Scale bar=30 μ m.

tured plants (6-8 vs. 1-6) (Figs. 7, 8). Th length, number and formation (dense or sparse) of peripherohaptera were variable under culture conditions. The peripherohaptera generally arose at the axial node where a lateral branch developed on the opposite side, but occasionally a peripherohapteron arose at an internodal site (Fig. 9). Once the filaments contacted with a substrate, a typical multicellular disc developed. New rhizoidal filaments also arose from the basal cells at the cut end of an erect shoot (Fig. 10).

Tetrasporophytes. Tetrasporangial stichidia were subapically produced on the upper parts of shoots (Fig. 11). In culture isolates from Japan, stichidia were 250-650 μ m (mean

Figs. 7-10. Peripherohaptera of B. simpliciuscula in field and culture. Fig. 7. A peripherohapterum at the axial node in a field plant from Nagara R. Note the peripherohaptera develops in tandem. Scale bar = $100 \mu m$.

Fig. 8. A peripherohapterum at the axial node in no. 752 isolate. Scale bar=200 μ m.

Fig. 9. A peripherohapterum at the internodal site in no. 520 isolate. Scale bar= $100 \mu m$.

Fig. 10. New rhizoidal filaments raised from the basal cells at the cut end of an erect shoot in no. 752 isolate. Scale bar = $100 \mu m$.

430 μ m, n=20) long and 120-250 μ m (mean 176 μ m, n=20) diam. with 4-7 tetrasporangia along axial cels (Fig. 12), whereas field tetrasporophytes had longer stichidia (150- 1300 μ m, mean 610 μ m, n=20) with 4-17 tetrasporangia along axial cels (Fig. 13). By contrast, the young stichidia of the Singapore culture isolate no. 2963 were mostly long (900-1900 μ m, mean 1280 μ m, n = 10) and after about three weeks growth they increased in length considerably (3.0-3.5 mm, mean 3.16 mm, $n = 5$). In the older stichidia, sporangia in the lower parts had already dis charged the spores, and new stichidia were progressively produced to their tips folowing the growth of axes.

Each axial cell near the apex cut off 4 or 5 pericentral cells outside, and then they divided longitudinaly and differentiated into a tetrasporangial mother cell on the upper side and a residual stalk cell (Figs. 14, 15). Tetrasporangia dividing tetrahedrally were 35-55 μ m (mean 46.3 μ m, n=15) in diam.

A stalk cell developed three primary cover cells toward the surface, and each primary cover cell produced 1 or 2 cover cells upward (Figs. 14, 15), rarely downward, too. These cover cells sometimes divided laterally in cultured plants (Fig. 14), but these lateral divisions were rarely seen in field plants (Fig. 15). The cover cels increased in number much more on intercalary stichidia that had already released tetraspores

Male gametophytes. Male plants usually developed their reproductive structures after the tetraspore germlings had become polysiphonous and branched. Some of them formed terminal spermatangial stichidia 400- $500 \mu m$ long directly from the monosiphonous axis of sporelings about 1.5-2.0 mm long. When the main axis became 2.5-3.0 mm long, it was polysiphonous and developd 2-4 secondary lateral branches with spermatangial stichidia (Fig. 16).

The spermatangial stichidia of the well developed plants were $375-850 \ \mu m$ long (mean

Figs. 11-15. Tetrasporophytes of B. simpliciuscula in culture and field.

Fig. 11. Tetrasporophytes with tetrasporangial stichidia (arrow) in no. 2963 isolate. Scale

bar=3 mm.
Fig. 12. A tetrasporangial stichidium in no.
752 isolate. Scale bar=100 μ m.

Fig. 13. A tetrasporangial stichidium in a

field plant from Nagara R. Scale bar= 100μ m.
Fig. 14. Surface view of a tetrasporangial stichidium in no. 752 isolate, showing a stalk cell (small arrow), a primary cover cell (large arrow) and secondary cover cells dividing upward (arrowhead) and laterally (double arrowhead). Scale bar= $50 \mu m$.

650 μ m, n= 14) and 60-85 μ m in diam. (Fig. 17). One or two stichidia often developed on each lateral and some became bifurcate. In spermatangial stichidia an axial cell produced four or five proximal pericentral cells per segment, and each proximal pericentral cell gave rise to 1-3 distal pericentral cells linearly or dichotomously (Fig. 18). Proximal and/or distal pericentral cels formed 1-5 cortical cels. Any superficial pericentral cels and cortical cels in a fertile branch could function as spermatangial mother cels, each cel producing 1-4 spermatia (Fig. 18). As evident in all other Bostrychia and Stictosiphonia species investigated in culture, spermatangia often were released en masse simultaneously from each stichidium.

Female gametophytes. Procarps were produced from the 4th to 12th axial cell of polysiphonous lateral branches. One to four procarps were usualy formed in series at the ventral side or occasionaly at the both sides. Each procarp consisted of a 4-celed carpogonial branch and a supporting cell (Fig. 19). Only one procarp with a 3-celed carpogonial branch was found in a cultured plant from Same River,]apan (Fig. 20). Trichogynes derived from the carpogonia were 30-225 μ m long and 5-7.5 μ m diam. Cystocarps developed subsphericaly (Fig. 21), being 140-480 μ m long and 130-480 μ m in diam. (Fig. 22). Each cystocarp possessed 6-7 longitudinal pericarp filaments and an ostiole (40-160 μ m diam.). The inner cells of gonimoblast were aligned straight toward the surface, producing tear-drop shaped or lanceolate carposporangia, 40-70 μ m long and 20- $35 \mu m$ in diam. Carpospores discharged from ostioles germinated in the same way as tetraspores.

Bisexual gametophytes. A few bisexual plants developed among the tetrasporelings of isolate no. 2963. These were similar in overall mor-

Fig. 15. Surface view of a tetrasporangial stichidium in a field plant from Nagara R., showing a stalk cell (small arrow), a primary cover cell (large arrow) and secondary cover cells dividing upward (arrowhead) and laterally (double arrowhead) Scale bar=50 μ m.

phology to the unisexual plants. Stichidia bearing procarps were adjacent to spermatangial stichidia (Fig. 23). Carposporophytes were formed and discharged carpospores that germinated normally. One plant which initially bore only male organs developed procarps for two months and then reverted back to a 100% male for the remaining two years. No mixed-phase plants of any other combinations with male or female reproductive organs and tetrasporangial stichidia were found.

Relative size of gametophytes. In isolate no. 2963 from Singapore the female plants were usually larger and longer than the males. Thirty-two 3-months old tetrasporelings from isolate no. 2963 showed the following size differences: females (range 1.0-2.2 cm long, mean 1.58 cm, $n = 18$), males (range 1.3-1.5 cm, mean 1.44 cm, $n=5$), bisexual (range 1.2-1.9 cm, mean 1.57 cm, $n=6$), vegetative $(range 1.5-1.7 cm, mean 1.6 cm, n=3).$ While this was a rather small sample set, it reflected the usual pattern observed in other cultured Bostrychia species in which males were smaller overall than females (e.g. B. tenella (Lamouroux) J. Agardh, West and Calumpong 1988).

Discussion

In culture condition, Bostrychia simpliciuscula was usually unisexual and showed the typical Polysiphonia-type life history pattern like other Bostrychia species, but a few bisexual plants with male and female reproductive organs developed among the tetrasporelings of the isolate no. 2963. These reproductive organs had the ability to produce normal carposporophytes. West and Calumpong (1988) reported bisexual and mixed-phase plants as well as unisexual ones of B. tenella under culture condition. Kumano (1988) reported that field-collected specimens of B . flagellifera $(=B.$ tenella ssp. flagellifera (Post) R.J. King et Puttock) had both procarps and spermatangial stichidia, and West (unpublished data) also obseved bisexual plants in B. pinnata J. Tanaka et Chihara. Though the occurrence of such bisexual plants seems not to be unusual in this genus, it is not sure whether these bisexual plants actually function in field or not, because nobody has ever reported field plants of Bostrychia bearing both cystocarps and spermatangial stichidia.

Tetrasporangial formation of the present species is fundamentally similar to those of the other Bostrychia species, but there are some differences among them in the formation of tetrasporangial cover cells. Firstly, in B. tenel la , the primary cover cell gives rise to cover cells both upward and downward (West and Calumpong 1988, Tanaka 1989), but in B . simpliciuscula most cover cells develop only upward as seen in B . moritziana (Sonder ex Kuetzing) J. Agardh (Kumano 1979) and B. radicans (Montagne) Montagne (Kumano 1979, Tanaka 1991). This tendency is com-

Figs. 16-23. Male, female and bisexual gametophytes and carposporophytes of B. simpliciuscula in culture. Fig. 16. An upper part of a plant in no. 436 isolate, showing spermatangial stichidia (arrow) borne on

lateral branches. Scale bar=500 μ m. Fig. 17. A spermatangial stichidium (arrow) in no. 2963 isolate, releasing many spermatia. Scale $bar = 200 \mu m$.

Fig. 18. Diagram of a part of spermatangial stichidium showing cell arrangement of a proximal pericentral cell (ppc), a distal pericentral cell (dpc), cortical cells (cc) and spermatia (s). Scale bar=20 μ m.

Fig. 19. A procarp consisting of a supporting cell (arrow), four carpogonial branches (arrowhead) and

trichogyne (double arrowhead) in no. 436 isolate. Scale bar=20 μ m.
Fig. 20. Diagram of a part of female gametophyte showing cell arrangement of three procarps. Note the procarp at the bottom consisting of a supporting cell, 3-celled carpogonial branch and trichogyne. Scale $bar=20 \mu m$.
Fig. 21. A female gametophyte bearing many cystocarps subterminally in no. 2963 isolate. Scale

 $bar=3$ mm.

Fig. 22. A mature cystocarp borne on a lateral branch including many carpogonia in no. 436 isolate. Scale

 $bar=100 \mu m$.
Fig. 23. A bisexual gametophyte in culture no. 2963 isolate. Procarps (arrowhead) on one branch and spermatangial stichidia (arrow) on adjacent branches. Scale bar=500 μ m.

mon in both field and cultured plants, so it may be useful as the additional characteristic to elucidate the phylogenetic relationship of this genus. Secondly, King and Puttock (1989) observed cover cells which divided laterally (they called as "partial cortication") in the field plants of B . simpliciuscula. We sometimes found such cover cells in the culture plants but rarely in the field plants, so the lateral division of cortical cells may be easily influenced by environmental conditions.

In spermatangial stichidia of Bostrychia species, the number and branching pattern of pericentral cells and cortical cells of this species are more variable than those of seven species reported by King and Puttock (1991). This species produces linearly or dichotomously 1-3 distal pericentral cells from a proximal pericentral cell as seen in B. tenella reported by Tanaka (1989), and each pericentral cell forms 1-5 cortical cells. As reported by King and Puttock (1991), the arrangement of cortical cells in the spermatangial stichidia is too variable to understand the taxonomic relationships within this genus.

Though the 4-celled carposporangial branches are common in Bostrychia species as well as all other members of Ceramiales, some authors reported the 3-celled carpogonial branches in several species of Bostrychia. Tanaka (1989) showed only 3-celled carpogonial branches in B. tenella, and Kumano (1988) also recognized that the 3-celled carpogonial branch was more common than the 4-celled one in B. flagellifera $(=B.$ tenella ssp. flagellifera). Both 3- and 4-celled carpogonial branches are also found in B . harveyi Montagne, B. pinnata, B. moritziana and B. tenella ssp. tenella by King and Puttock (1989). West and Calumpong (1988) reported that B. tenella produced 2-, 3- and 4-celled carposporangial branches in culture condition and that 3-celled ones were seen more frequently than 2- or 4-celled ones. In the present species, most carpogonial branches are 4-celled and only one 3-celled carpogonial branch was observed. As pointed out by Tanaka (1991), 3-celled carpogonial branches may not be unusual in Bostrychia species.

Since these results were taken from observations only on the field plants except for West and Calumpong (1988) and the present study, the further studies based on the cultured plants will be necessary for getting the precise cell numbers of carpogonial branches and for elucidating the developmental sequence of carpogonial branches in each taxon.

In field plants, there were not remarkable differences of the gross morphology among Japanese, Australian and Singapore localities. Only Shiira River's plants had long and sparse peripherohaptera, though plants in other localities had short and dense ones. Such long and sparse peripherohaptera had been reported in this species from Kagoshima, southern]apan (Tokida 1939). Under cuture condition, however, the morphology of peripherohaptera was quite variable, and some isolates with short and dense peripherohaptera formed long and sparse ones. Therefore, this morphological feature may be induced by a certain environmental condition. In cultured plants, tetrasporangial stichidia of] apanese isolates were shorter than those of Singapore ones. This difference may be also induced from the difference of culture condition because long stichidia were often found in]apanese field plants.

Bostrychia simpliciuscula showed the Polysiphonia-type life history under laboratory culture, but very few fertile gametophytes could be collected in field. It is still uncertain whether this species has a sexual life history in field or is dispersed by vegetative growth and fragmentation in order to extend and maintain its distribution. Considering that we could find tetrasporophytes with stichidia from only 5 of 27 localities, this species may disperse mainly by vegetative growth and fragmentation rather than discharging tetraspores and carpospores. Molecular taxonomic techniques, such as isozyme analysis or RFLPs of gene molecules, would be useful for resolving these problems, because they can clarify whether this species is genetically diverse or not.

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神谷充伸*· John A. West** · 原慶明*: 紅藻タニコケモドキ(イギス目) の天然および培養下における生殖体の構造

日本・シンガポール・オーストラリア産タニコケモドキ (Bostrychia simpliciuscula) の天然および培養で得られた 生殖藻体の形態を詳しく記載した。雌雄配偶体および果胞子体の記載は初めてである。本藻は通常雌雄異株のイ トグサ型生活史であったが,シンガポール株から放出された四分胞子の発芽体には雌雄同株のものが含まれてい た。造果枝は主に 4細胞を基本とするが,まれに 3細胞のものも観察された。不動精子托の皮膚細胞の数や分裂 様式はコケモドキ属の他種に較べてより変異に富んでいた。 (*305茨城県つくば市天王台1-1-1 筑波大学生物 科学系 **School of Botany, University of Melbourne, Parkville, Victoria 3052 AUSTRALIA)

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