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Notes on Reproduction in *Rhodochorton purpureum* (Lightfoot) Rosenvinge (Rhodophyta) with Special Reference to Hokkaido Plants

Lee, Yong-Pil

(Department of Biology, Cheju National University, Cheju)

日本 北海道産 紅藻 *Rhodochorton purpureum* (Lightf.) Rosenvinge의 生殖에 關한 註解

李 龍 弼

(濟州大學校 理工大學 生物學科)

ABSTRACT

Observations on reproduction of *Rhodochorton purpureum* (Lightfoot) Rosenvinge (Acrochaetiaceae, Rhodophyta) was carried out with plants from Hokkaido, Japan. This species produces no monosporangia both in nature and culture, even though it does tetrasporangia commonly. The plants from Nemuro produce neither sporangia nor gametangia, and thus vegetative reproduction is the only known way to propagate themselves. It is suggested that the vegetative reproduction occurs in nature by fragmentation of vegetative filaments after development of a rhizoid. Several different modes of rhizoid production are described. The plants from Akkeshi and Oshoro (I) produce tetrasporangia that develop into plants producing only tetrasporangia. The plants from Muroran and Oshoro (II) produce tetrasporangia that develop into gametophytes. Gametophytes of *R. purpureum* from Muroran produce tetrasporangia as well as spermatangia or carpogonia. Such tetrasporangia on gametophytes are presumed to be mitotic.

INTRODUCTION

Since *Rhodochorton purpureum* (Lightfoot) Rosenvinge was described from the Island of Iona, Scotland as *Byssus purpurea* Lightfoot (1777), tetrasporangia have been the only reproductive structure known from the field. Male and female gametophytes were reported under culture conditions by Knaggs (1968). West (1969) described a life history with unisexual gametophytes from California plants. The same results were reported also in the Netherlands (Stegenga, 1978) and Hokkaido (Ohta and Kurogi, 1979). Bisexual gametophytes from Chile (West, 1970b) and Hokkaido (Ohta and Kurogi, 1979) were isolated and shown the same life history as unisexual ones.

Baardseth (1941) observed bisporangia on the plants from Tristan da Cunha and described the plants as *R. bisporiferum.* Klavestad (1957) observed parasporangia on the plants from Tvaerminne, Finland. However, the function of such sporangia (bi- and parasporangia) was not known. The possibility of vegetative reproduction was suggested by Rosenvinge (1900), Knaggs (1966), and Pearlmutter and Vadas (1978).

Field-collected and cultured material from Hokkaido are observed to draw conclusions on the probable means of reproduction in nature in different population of *R. purpureum.*

MATERIALS AND METHODS

Plants were collected on the coast of Hokkaido, Japan as follows: Akkeshi plants at the littoral fringe in Daikokuzima July 2, 1977, Nemuro plants at the eulittoral zone in Bentenzima June 2, 1977, Muroran plants at the eulittoral zone in Nirasu June 9, 1978, Oshoro (I) plants at the littoral fringe in Oshoro Bay May 9, 1979, and Oshoro (II) plants at the littoral fringe and eulittoral zone in a maritime cave May 9, 1978. Part of each collection was cultured in the Laboratory of the Department of Botany, Faculty of Science, Hokkaido University. The details of the culture work are described elsewhere (Lee and Kurogi, 1983). The material collected in fields was examined under microscope after fixation with 5% formalin seawater. Slide specimens are deposited in the Herbarium of the Department of Biology, Cheju National University, Korea.

OBSERVATIONS

Vegetative reproduction. Nemuro plants bore no tetrasporangia when collected. The plants also produced no tetrasporangia under the culture conditions. Erect filaments of the plants were mixed with rhizoids* and fragments of vegetative filaments in nature. Some creeping filaments** were free from the massive basal system and mixed with erect filaments. The plants produced rhizoids on erect filaments in both nature and culture (Figs 4, 6). The rhizoids are easily distinguished from erect filaments by their more sharply tapering distal ends, by their flexuous profile, and by their laterals formed by a fork-like protrusion (Fig. 5). The rhizoids developed at various angles, such as from obtuse to acute or sometimes creeping along the main axis. Occasionally, the apical part of a main axis was transformed into a rhizoid (Fig. 1).

Frequently, rhizoids arose on erect filaments by an intercalary mode, sharing the cell contents of their mother cells (Figs 3, 8, 9). Part of the cell contents of the mother cell

* The word "rhizoid" is used here to indicate the multicellular filaments developing on indefinite parts of erect filaments and having a function to anchor the thallus as a kind of basal system.

** The word "creeping filament" is used to indicate the filaments developing from the base of a thallus and forming a basal system.

migrated into the initial tube of the rhizoid, resulting in a partial lumen in the mother cell. Then the cell adjacent to the lumen gave rise to another new filament, either an initial of a rhizoid or of an erect filament.

Plants from Nemuro showed several different ways of fragmentation of thalli instead of production of sporangia or gametangia for self-propagation. Some probable ways of vegetative filaments in nature are summerized as follows (Fig. 23):

A) An intercalary rhizoid developing on an erect filament attaches to other erect filament and causes one of the erect filaments to be severed by environmental forces.

B) As a rhizoid develops from the most proximal cell of a branch on an erect filament, the original pit-connection between the most proximal cell of the branch and the cell of the erect filament disappears, resulting in the separation of the branch from the erect filament (also see Fig. 6).

C) When a cell of an erect filament gives rise to a new intercalary filament, part of the cell contents migrates into the initial of the new filament, leaving part of the cell empty (also see Figs 8, 9). The cell adjacent to the lumen in the other part of the filament gives rise to another filament in the lumen. The lumen is broken apart by the growth of the two new filaments and by environmental forces (also see Fig. 3).

D) An erect filament issues a new filament from each of two contiguous cells by means of intercalary regeneration. The original pit-connection between the two cells disappears, and a form like the false branching of blue-green algae results (also see Fig. 7). The portion between the cells issuing new filaments is broken by environmental forces.

E) Creeping filaments free from a basal system can become entangled in or attached to other filaments or the substrate. Thus, the creeping filaments are easily broken by environmental forces.

Some fragments of erect filaments showed no polarity when regenerating because they gave rise to rhizoids at both severed ends (Fig. 2). Although no fragments in observed material gave rise to erect filaments from both severed ends, Pearlmutter and Vadas (1978) reported such a case under culture conditions.

Tetrasporangia. In nature the plants from Akkeshi bore no tetrasporangia when collected. Plants from Muroran, Oshoro (I), and Oshoro (II) bore tetrasporangia in the apical region of erect filaments when collected. In Muroran plants there were tetrasporangia borne on one- to three-celled stalks which developed on creeping filaments that were free from the basal system (Fig. 10). Most tetrasporangia in the field-collected material were abortive. Occasionally, germinating spores postulated to be the tetraspores of *R. purpureum* were observed.

Plants from all localities but Nemuro produced tetrasporangia under the culture conditions. Also, tetrasporangia occurred on one- to three-celled stalks that developed on creeping filaments as in nature (Fig. 22). However, no plants bearing sexual reproductive structures occurred in the culture vessels of Akkeshi and Oshoro (I) plants.

Tetraspores produced by Oshoro (II) plants germinated and developed into unisexual gametophytes. Some of the gametophytes showed good vegetative growth; they were usually sterile or often tetrasporiferous. Spermatangia rarely appeared in small clusters at the apex of erect filaments on such gametophytes (Fig. 17). All tetrasporangia but for a few aberrant ones on the gametophytes were abortive before or after the first division of the tetrasporangium.

The gametophytes derived from the tetraspores of Muroran plants were also unisexual. At early developmental stages, they could be distinguished into five types in regard to the production of reproductive structures under 10 °C long day (16:$\bar{8}$) culture conditions: 1) plants bearing only spermatangia (Fig. 13), 2) plants bearing only carpogonia (Fig. 11), 3) plants bearing only tetrasporangia (Fig. 15), 4) plants bearing both tetrasporangia and spermatangia (Fig. 16), 5) plants bearing both tetrasporangia and carpogonia (Fig. 19). It was not determined whether or not the plants bearing only spermatangia or carpogonia produce tetrasporangia as well latter in their development. However, the plants bearing only tetrasporangia produced carpogonia or spermatangia exclusively when the plants were isolated in other culture vessels even under the same conditions as before. Tetrasporangia borne on the gametophytes usually underwent a first division by a transverse wall only or occasionally a second division in a cruciate mode.

Spermatangia, carpogonia, and sexual reproduction. Although unisexual plants only were observed in this study, Ohta and Kurogi (1978) isolated bisexual plants from the material collected in Oshoro Bay. Spermatangia in the unisexual plants were borne in hemispherical to spherical clusters on short erect filaments (Figs 13, 16). Carpogonia were borne on the cells of erect or creeping filaments, or even on persistent germinating spores (Fig. 12). A fertilized carpogonium elongates distally and increases in width (16-24 μm wide and 130-170 μm long, Fig. 14). Then it divided with transverse walls into three to five cells

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Fig. 1. Erect filaments of Nemuro plants. Note that rhizoids (R) are transformed from the upper part of an erect axis (arrow) or developing from the most proximal cell of a branch. scale=100μm

Fig. 2. Fragment of an erect filament with rhizoids from both severed ends (Nemuro plants). scale=100μm

Fig. 3. Rhizoid developing from an intercalary cell (arrow; Nemuro plants). scale=50μm

Fig. 4. Rhizoids (R) developing on an erect filament (Ef) (Nemuro plants). scale=100μm

Fig. 5. Branching mode of rhizoids (Nemuro plants). scale=30μm

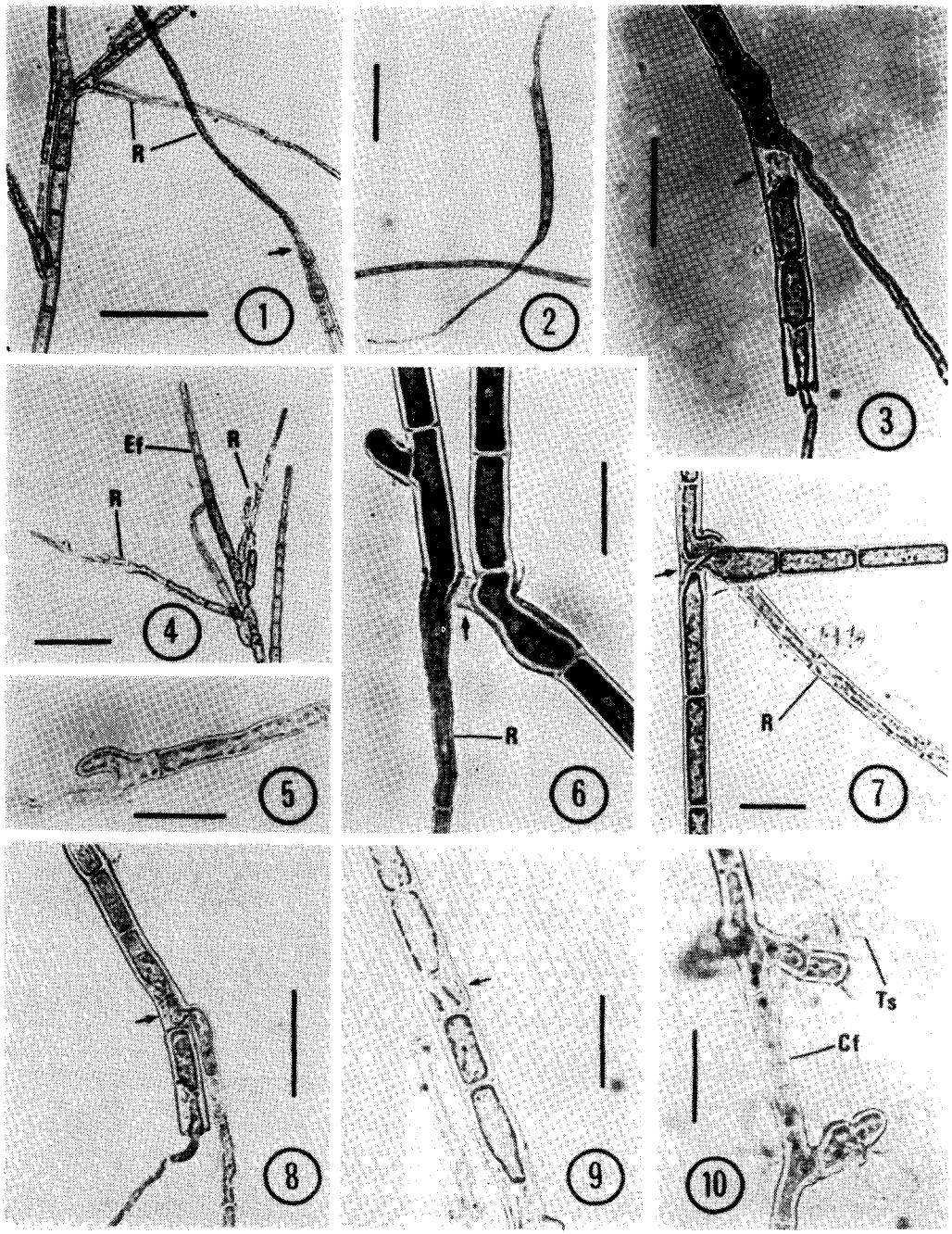
Fig. 6. Rhizoid developing from the most proximal cell of a branch. Note the part of the cell becoming an empty lumen (arrow; Nemuro plants). scale=30μm

Fig. 7. Both a part of new erect filament and a rhizoid (R) developing by an intercalary mode. Note the false branching form (arrow; Nemuro plants). scale=30μm

Figs 8, 9. Rhizoids developing by an intercalary mode (arrow: Nemuro plants). scale=50μm

Fig. 10. Empty tetrasporangia (Ts) borne on a free creeping filament (Cf) (Muroran plants). scale=30μm

*Illustrations (#1-5, 7-10, 18) are of field-collected material, whereas the rest (#6, 11-17, 19-22) are of cultured material.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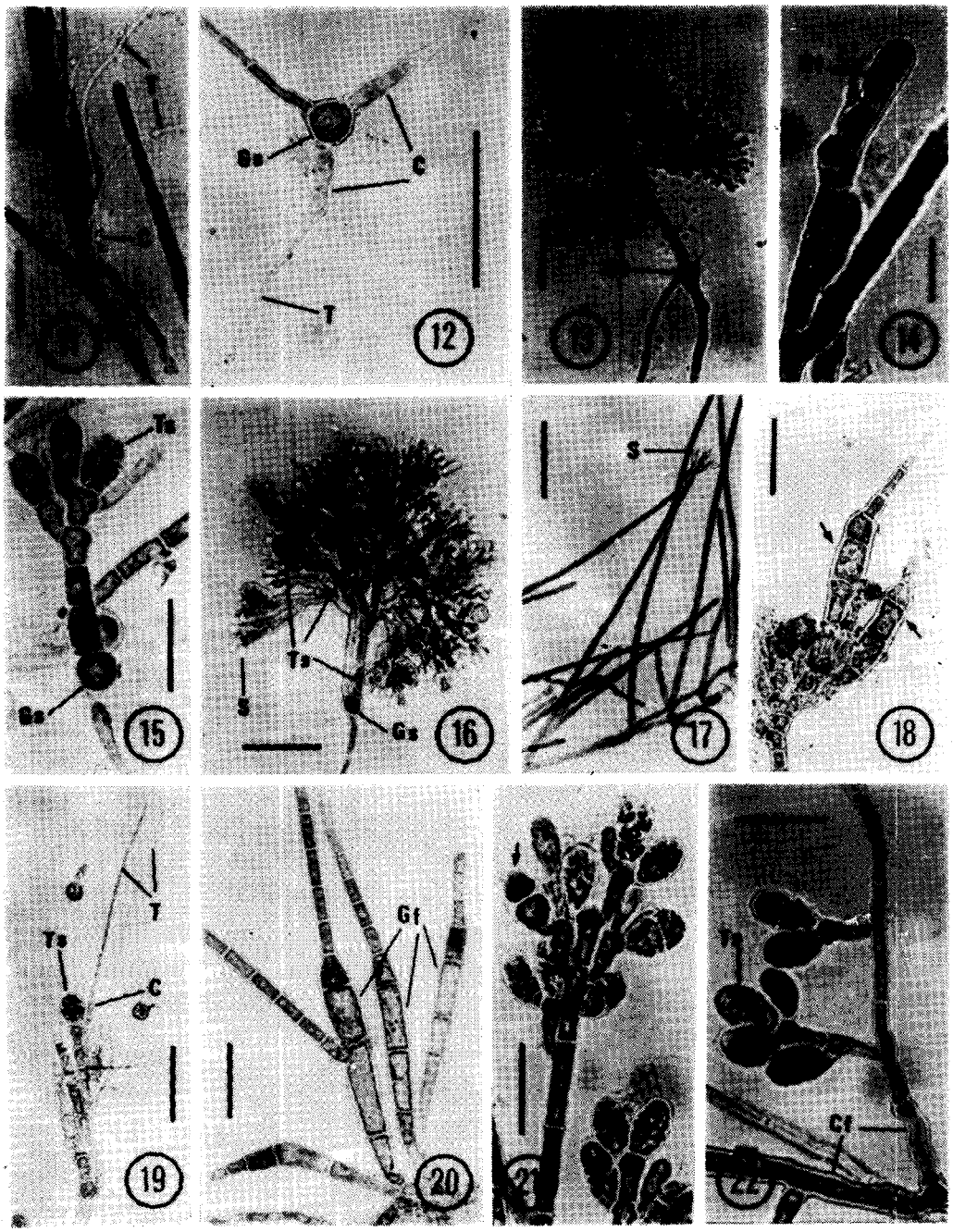
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forming a club-shaped gonimoblast filament*, issuing creeping filaments from its basal cell. New gonimoblast filaments arose around the base of the first ones, resulting in a tuft of gonimoblast filaments (Fig. 20). The apical or an intercalary cell of the gonimoblast filaments issued a narrow filament. Such narrow filaments issued branches, which became carpotetrasporophytes and produced carpotetrasporangia when mature, being similar in morphology to the erect filaments of gametophytes or of plants in nature. Carpotetraspores also germinated and developed into a gametophyte like the tetraspores from Muroran and Oshoro (II) plants did.

Although on a specimen from Oshoro (II) plants gonimoblast-like filaments were observed in nature (Fig. 18), it was not confirmed whether the filaments were actually homologous to the gonimoblast filament derived from a fertilized carpogonium as observed in culture.

Other sporangia. No plants bore monosporangia among the plants examined in nature or culture. Occasionally, some aberrant sporangia which include 1~4 globular bodies were observed both in nature and in culture (Fig. 21). The globular bodies contain rather denser cell contents than those of a normal sporangium. Although some of the bodies in the aberrant sporangia exhibited *in situ* germination, no released ones were confirmed. Some aberrant sporangia including two bodies were similar in shape to bisporangia (*sensu* Baardseth 1941). No parasporangia (*sensu* Klavestad, 1957) were observed.

DISCUSSION

Rosenvinge (1900) reported intercalary regeneration and fragments with rhizoids in *R.*

Fig. 11. Female gametophyte bearing only carpogonia (C) with long trichogynes (T) (Muroran plants). scale=50μm
Fig. 12. Carpogonia developing on a germinating spore (Gs) (Muroran plants). scale=50μm
Fig. 13. Male gametophyte bearing only spermatangia (Muroran plants). scale=50μm
Fig. 14. Gonimoblast filament (Gf) at the beginning of the post-fertilization development (Muroran plants). scale=20μm
Fig. 15. Gametophyte bearing only tetrasporangia (Muroran plants). scale=30μm
Fig. 16. Male gametophyte bearing both spermatangia (S) and tetrasporangia (Ts) (Muroran palnts). scale=50μm
Fig. 17. Thallus bearing a small cluster of spermatangia (S) (Oshoro (II) plants). scale=100μm
Fig. 18. Branches showing early gonimoblast development (arrows; Oshoro (II) plants). scale=50μm
Fig. 19. Female gametophyte bearing both carpogonia (C) and tetrasporangia (Ts) (Muroran plants). scale=50μm
Fig. 20. Gonimoblast filaments issuing terminal and/or lateral (arrows) carpotetrasporphytic filaments (Muroran plants). scale=50μm
Fig. 21. Aberrant sporangium including two bodies (arrow; Akkeshi plants). scale=30μm
Fig. 22. Tetrasporangia (Ts) developing on creeping filaments (Cf) (Akkeshi plants). scale=30μm

* The word "gonimoblast filament" is used here to indicate the thick, three- to five-celled and club-shaped filament, which develops from a fertilized carpogonium.

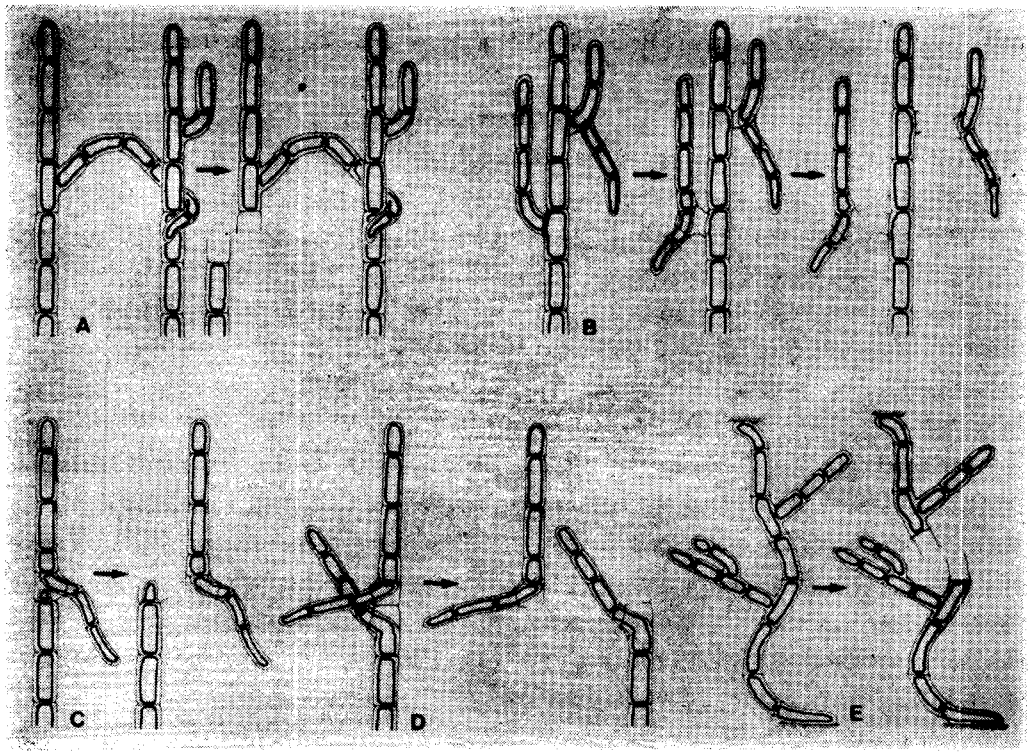

Fig. 23. Diagramatic explanation of five possible modes of fragmentation of vegetative filaments (see text).

purpureum (described as *R. islandicum* Rosenvinge). He stressed the importance of fragments with rhizoids for the propagation of the plants. Knaggs (1966) considered two modes of fragmentation in *R. purpureum*: fragmentation by death of an intercalary cell (i.e., by external effects) and autofragmentation by intercalary meristematic activity that gives rise to appendant branches or rhizoids rather than contributing to the increase in length of the main axis (i.e., by internal effects). Pearlmutter and Vadas (1978) supported through culture experiments the possibility of the vegetative reproduction in *R. purpureum* in nature, which have been suggested by these earlier workers and by West (1974).

Under stationary culture conditions Nemuro plants gave rise to numerous rhizoids on erect filaments, although fragmentation of vegetative filaments did not occur as in nature. Therefore, like Knaggs' autofragmentation, the intercalary development of rhizoids on erect filaments is mediated by internal (physiological) factors rather than external (mechanical) ones such as wave action etc., although the latter factors may provide the stimulation. Furthermore, it seems reasonable to expect that erect filaments may be fragmented in nature after some rhizoidal development has occurred rather than rhizoidal development following the fragmentation.

In culture the plants from Akkeshi and Oshoro (I) produced numerous tetrasporangia

and released tetraspores, but no plants bearing sexual reproductive structures were observed. West (1969) reported the same situation for the plants from Washington and Alaska. The gametophytes derived from Muroran plants produced many tetrasporangia exclusively or together with spermatangia or carpogonia. Stegenga (1978) found tetrasporangia on some gametophytes of *R. floridulum* (Dillwyn) Naegeli in culture but thought them to be functionless.

Conway and Knaggs (1966) reported the tetrasporangia of *R. purpureum* from Shetland were meiotic. West (1969) postulated that meiosis occurs in the carpotetrasporangium of *R. purpureum*, but that *R. concrescens* Drew produces mitotic tetrasporangia (West, 1970a). Thus, it is postulated that mitotic tetrasporangia may also be formed on gametophytes of *R. purpureum* and have a role in self-propagation of the gametophytes. Cytological studies are needed to determine whether meiosis or mitosis occurs in the tetrasporangia on gametophytes and also whether mitotic tetrasporangia might not be formed on carpotetrasporophytes of *R. purpureum*.

In culture, as a tuft of carpotetrasporophytes derived from a fertilized carpogonium of *R. purpureum* mature and develop more creeping filaments on the female gametophyte, the thallus of the latter finally gives way to that of the former. The female gametophyte, as a result, becomes difficult to be recognizable. The male gametophyte keeps growing vegetatively as an independent individual, since no substituting plants develops on it. It is postulated by the fact that the thallus of the male gametophyte of *R. purpureum* may grow up with a morphology similar to a carpotetrasporophyte and produce tetrasporangia dominantly rather than spermatangia under certain physiological or environmental conditions in nature. Then, it is also considered possible that the male gametophyte of *R. purpureum* may be overlooked in nature because observers can confuse it with the carpotetrasporophyte when spermatangia are lacking. On the other hand, it can be expected that some thalli bearing both tetrasporangia and spermatangia as in Figs 16 and 17 will be found at certain localities. Specimens of some species of *Rhodochorton* bearing both tetrasporangia and spermatangia in nature have in fact been described: *R. spetsbergense* (Kjellman) Kjellman (Rosenvinge, 1923~1924), *R. floridulum* (Dillwyn) Naegeli (Knaggs, 1965) and *R. membranaceum* (Magnus) Hauck (unpublished data of the author).

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摘 要

紅藻 *Rhodochorton purpureum* (Lightf.) Rosenvinge의 生殖에 關한 硏究를 日本 北海道産 植物을 중심으로 하여 수행하였다. 이 種은 주로 四分胞子囊을 形成하지만 單胞子囊은 自然狀態나 實驗室조건에서도 形成하지 않는다. Nemuro産 植物은 胞子囊이나 配偶子囊을 形成하지 않고 營養生殖에 의한 번식을 하고 있다. 自然狀態에서 營養生殖은 絲狀體의 一部에 假根이 形成된 후에 그 部分이 떨어져나가 새로운 個體로 된다. Akkeshi와 Oshoro産(Ⅰ) 植物에서 形成된 四分胞子는 四分胞子를 形成하는 植物體로 發達한다. 그러나 Muroran과 Oshoro産(Ⅱ) 植物에서 形成된 四分胞子는 配偶體로 發達하는데, 이들 配偶體는 四分胞子囊과 雄性 또는 雌性配偶子囊을 形成하므로 配偶體에 形成되는 四分胞子囊은 有絲分裂에 의해서 形成되었으리라 생각한다.

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