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Culture studies on *Caulerpa* (Caulerpales, Chlorophyceae) I. Reproduction and development of *C. racemosa* var. *laetevirens*

Sachito ENOMOTO and Hideo OHBA*

Marine Biological Station, Faculty of Science, Kobe University, Iwaya, Awaji-cho, Hyogo-ken, 656-24 Japan

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Reproduction and development of the marine green alga *Caulerpa racemosa* var. *laetevirens* from two localities of the southern part of Japan were studied in laboratory culture experiments.

Wild mature plants collected during May and July and kept in autoclaved seawater produced gametes within about one month in culture under the following conditions: 25°C, 1.0–3.0 klux, and 14L/10D cycle.

Both sexes of biflagellate gametes were produced in the same plant. Gametes are anisogamous. A stigma was found in the relatively large female gametes, but not in the relatively small male gametes. Copulation was observed between gametes from the same plant. Settled zygotes became spherical and increased their volume for five weeks while retaining their spherical shape.

After five weeks, each spherical germling attained a diameter of about 120 μm and formed two germ tubes bipolarly. A fine primary germ tube was formed on the side away from the light. After about a week a thick secondary tube was formed on the side facing the light. Both tubes elongated and branched, resulting in creeping, filamentous, protonema-like plants. These creeping plants formed thick primary shoots which differentiated into creeping rhizomes and upright shoots.

The upright shoot formed ramuli and developed into an assimilator. Three types of assimilators were produced under different culture conditions —*laetevirens*-type under 20.0°C, 5.0 klux, *peltata*-type under 25.0°C, 1.5 klux, and intermediate-type under 20.0°C, 1.5 klux or 25.0°C, 5.0 klux. After 4–5 months, germlings developed into mature plants. After 5–6 months, they became fertile and produced both male and female gametes on the same plant. No quadriflagellate or stephanokontic zooids were observed.

Key Index Words: Caulerpa, Caulerpa racemosa *var.* laetevirens, *Caulerpales, Chlorophyceae, culture, development, life-history, reproduction.*

The coenocytic marine green alga *Caulerpa* is widely distributed in the littoral and sublittoral waters of tropical and subtropical seas. Several species are utilized as food, and mariculture has been started in some Asian countries.

Much information concerning the structure of the gametangium and the copulation of gametes in *Caulerpa* has accumulated from the work of many investigators (MONTAGNE 1838, DERBÈS & SOLIER 1850, WEBER-VAN BOSSE 1898, DOSTÁL 1928a, 1928b, 1929, SCHUSSNIG 1929a, 1929b, 1939, SCHWARTZ & SCHWARTZ 1930, ARWIDSSON 1930, ERNST 1931, IYENGAR 1933, 1940, YAMADA 1934, MIYAKE & KUNIEDA 1937, HAGIHARA & HIROSE 1969, KAJIMURA 1969, 1970, 1976, 1977, and GOLDSTEIN & MORRALL 1970). GOLDSTEIN & MORRALL (1970) gave a historical review of these results. However, the development of the thallus of *Caulerpa* has been reported preliminarily in only two species, *C.*

* Present address: Laboratory of Phycology, Tokyo University of Fisheries, Konan, Minato-ku, Tokyo, 108 Japan.

serrulata from Australia (PRICE 1972) and *C. okamurae* from Japan (ISHIWARA *et al.* 1981).

Our research concerns the reproduction and development of several species of *Caulerpa* in laboratory culture experiments. The present paper presents the results of our studies of *C. racemosa* var. *laetevirens* from two localities of the southern part of Japan.

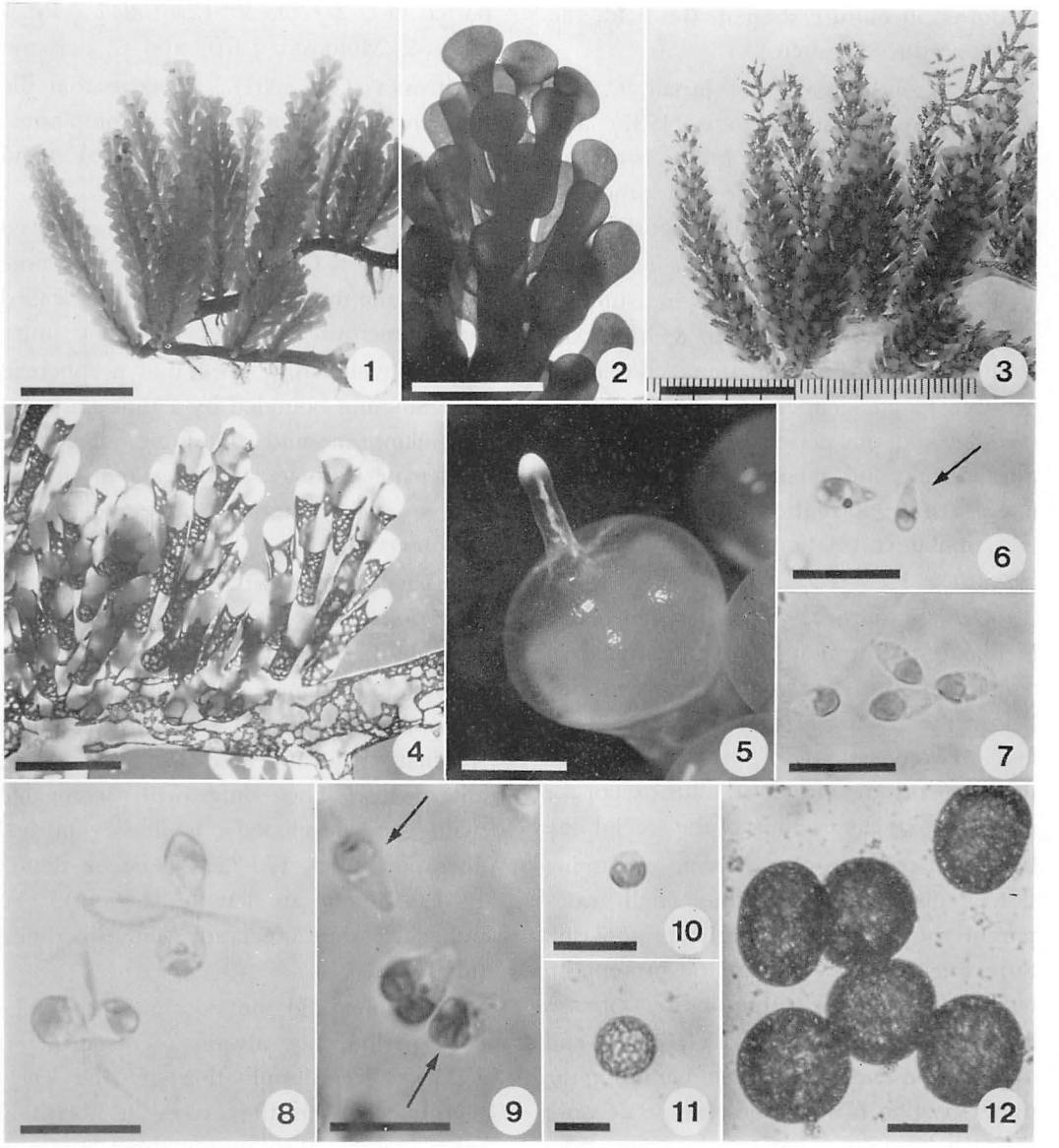
Materials and Methods

Plants of *Caulerpa racemosa* var. *laetevirens* were collected from the lower part of the littoral zone at Muroto-misaki (33°16'N, 134°14'E) in Shikoku and the upper sublittoral zone in the outer fringe of coral reef flats at Ayamaru-misaki (28°28'N, 129°43'E) in Amami-ôshima. The collections were made from May to July of 1981–1985. Materials were kept at 13–15°C and immediately brought to the laboratory. After the fronds were freed from epiphytes and small animals, they were rinsed with filtered (Toyo filter paper No. 4A and No. 5C) and autoclaved (125°C, 20 min) seawater. Each frond was placed in a separate glass vessel containing 350 m*l* of sterilized seawater. For prevention of the luxuriant growth of algal epiphytes, no nutrients were added. The seawater was changed every 5 days. The plants were kept under 25°C, 1.0–3.0 klux, 14L/10D (06:00–20:00L/20:00–06:00 D) cycle. Gametes were discharged about one month after the beginning of preculture, in the early morning within 1–2 hr after illumination. They were discharged through liberation tubes as a highly viscous, dark green material, which precipitated onto the bottom of the vessel. With a slight agitation of the medium, male and female gametes swarmed out from the viscous material and immediately copulated. About 0.5 m*l* of suspension of zygotes was diluted with 300 m*l* of sterilized seawater. One or two drops of diluted suspension were inoculated into screw-capped glass tubes containing 15 m*l* of PROVASOLI's ES medium (prepared according to MCLACHLAN, 1973) with a micropipette. In another series of experiments, one or two drops of the suspension were inoculated onto glass coverslips (20 $\times 20 \times 1$ mm) covered with 1 m*l* of seawater, and placed in petri dishes. The zygotes attached themselves to the coverslips within 30 min, whereas uncopulated gametes continued swimming. An hour after being placed in petri dishes, the coverslips were rinsed with running seawater to remove the uncopulated gametes and then transferred into glass vessels (60 mm diam., 90 mm high) containing 150 m*l* of the same medium. These coverslips were used for observation of zygote development. Zygotes were cultured at first under the above-mentioned conditions. When germlings grew to 1–2 mm in length, they were isolated and transplanted into separate glass tubes. Two months after inoculation, germlings had grown to 10 mm in length and then were transferred into glass vessels (90 mm diam., 90 mm high) containing 350 m*l* of the same medium. These vessels were placed under the following four conditions: 1) 20.0°C, 1.5 klux; 2) 20.0°C, 5.0 klux; 3) 25.0°C, 1.5 klux; and 4) 25.0°C, 5.0 klux. A daylength of 14 hr (06:00–20:00) was employed. In the field, the present alga appeared luxuriantly in April-May and gradually disappeared in July-August. The water temperature of the habitats in April was about 20°C and that of July about 25°C. The culture medium was changed every 2 weeks. Cultures were not axenic, but they were strictly unialgal.

For light microscopy, gametes were fixed in 4% seawater glutaraldehyde.

Results and Discussion

1. *Maturation of plants*: Within about



Figs. 1–12. Reproduction of *C. racemosa* var. *laetevirens*. 1. Mature vegetative plant from Murotomisaki. 2. A part of a vegetative assimilator. 3. Fertile plant with protoplasmic networks, one day before liberation. 4. Protoplasmic network in fertile assimilator. 5. Liberation tube on a ramulus. 6. Biflagellate male gamete (arrow). 7. Biflagellate female gametes. 8. Copulation of gametes. 9. Heart-shaped planozygote and completely copulated quadriflagellate planozygotes (arrows). 10. Settled zygote, after 3 hr copulation. 11. Spherical body, after 15 days. 12. Spherical bodies increasing cell volume, after 24 days. Scale: (Figs. 1, 3)=20 mm, (Figs. 2, 4)=5 mm, (Fig. 5)=1 mm, (Figs. 6–10)=10 μm, (Fig. 11)=20 μm, (Fig. 12)=50 μm.

one month after the beginning of the laboratory culture, vegetative plants from the field (Figs. 1 and 2) became fertile under 25.0°C, 1.0–3.0 klux, 14L/10D conditions. Although the light intensity was far lower in culture than in the field, the plants produced gametes.

In the southern part of Japan, *C. brachypus* (MIYAKE & KUNIEDA 1937) and *C. okamurae* (KAJIMURA 1969, ISHIWARA *et al.* 1981) became fertile and produced gametes during July and August. Our results suggest that *C. racemosa* var. *laetevirens* also becomes fertile in summer (June and July). GOLDSTEIN & MORRALL (1970) observed an apparent correlation between gametogenesis in some Caribbean *Caulerpa* and the period of extreme spring tides during full moon. Our study does not provide information on whether there is a similar correlation in *C. racemosa* var. *laetevirens*.

2. *Gamete formation*: The first sign of the incipient maturation of plants was recognized in the evening of the third day before the liberation of the gametes as a loss of homogeneity of protoplasmic distribution throughout the thallus except for rhizoids. In the evening of the second day before liberation, protoplasmic streaming slowed down and numerous small transparent spots appeared in the protoplasm. Subsequently, the spots in the protoplasm enlarged and the protoplasmic masses formed an irregular network (Figs. 3 and 4). In the evening before liberation, the upper portion of the protoplasmic network of each ramulus changed in color from green to dark yellowish-green, while the networks of lower portions of ramuli, upright shoots and rhizomes remained green. Just before liberation, the contrast between the colors of the network increased. By dissection, it was confirmed that the male gametes were formed in the green portion, while the female gametes, each of which had a reddish stigma, were formed in the dark yellowish-green portion. Such a sexual localization in a frond has been reported in *C. cupressoides*, *C. serrulata* (GOLDSTEIN & MORRALL 1970) and *C. okamurae* (ISHIWARA *et al.* 1981). It seems that the difference in color of the protoplasmic networks is caused by the reddish stigmata in female gametes.

GOLDSTEIN & MORRALL (1970) observed that in some Caribbean *Caulerpa* a large cytoplasmic mass of the erect frond cleaved into numerous smaller cytoplasmic units, each of which developed into a spherical gametangium bounded by a thin gametangial membrane and containing either male or female gametes. During our investigation, such spherical gametangia were not observed.

3. *Gamete liberation*: The formation of liberation tubes (papillae) started in the evening of the second day before liberation at the apical portions of upright shoots, the upper surfaces of ramuli and rhizomes. At first they appeared as tiny whitish outgrowths. The outgrowths elongated swiftly and developed into fine cylindrical liberation tubes, 170-220-250 μm in diam., 1.0-1.5-1.8 mm in length (Fig. 5). No trabeculae were observed in any liberation tube.

Liberation did not occur during the dark period, but always occurred about 1–2 hr after illumination in the early morning. When the apices of liberation tubes burst, the protoplasmic network broke down rapidly into dark green viscous material. The viscous material liberated through the liberation tubes and precipitated on the bottom of the vessel. Liberation continued for about 15 min, the mother plant losing its contents and fading. Nu-

merous gametes swam out from the viscous material with a slight agitation of the medium.

Liberation in the early morning was reported also in *C. brachypus* (MIYAKE & KUNIEDA 1937) and *C. okamurae* (ISHIWARA *et al.* 1981). It was possible to postpone liberation two or three hr by extension of the dark period. These facts suggest that illumination probably triggers liberation.

4. *Male and female gametes*: Two types of gametes were recognized. One (male) was relatively small, 4.5–6.0 μm in length, and 2.0–2.5 μm in breadth, and lacked a stigma (Fig. 6). The other (female) was larger, 5.5–7.5 μm long and 2.5–3.0 μm broad, and contained a reddish stigma (Fig. 7). Both sexes of gametes were biflagellate, 7.5–10.0 μm long, and tear-drop-shaped or slender pear-shaped, being pointed at the anterior and rounded at the posterior. They showed a weak positive phototactic response. The motion of the female gamete was rather slow, while the male gamete was more active. The swimming period of female gametes was shorter than that of male gametes.

The present alga always produced both sexes of gametes on the same frond and therefore is considered to be monoecious. Other monoecious taxa of *Caulerpa* that have been reported are *C. racemosa* var. *uvifera* (IYENGAR 1940), *C. mexicana*, *C. racemosa*, *C. serrulata*, *C. sertularioides*, and *C. taxifolia* (GOLDSTEIN & MORRALL 1970), and *C. okamurae* (ISHIWARA *et al.* 1981), while dioecious taxa include *C. clavifera* (ERNST 1931) and *C. brachypus* (MIYAKE & KUNIEDA 1937). Concerning *C. prolifera*, SCHUSSNIG (1939) reported that the Mediterranean plants were dioecious, while GOLDSTEIN & MORRALL (1970) described the Caribbean plants as monoecious.

5. *Copulation and zygotes*: When the gametes swam out from the viscous mass, males copulated with females and became quadriflagellate planozygotes, each with two chloroplasts and a stigma (Figs. 8 and 9). The planozygotes had a weak negative phototactic response and swam vivaciously at first, then gradually slowed down and came to rest on the substratum, becoming spherical (Fig. 10). Within a few hours after settling, zygotes had become completely spherical and their flagella had disappeared. Twenty-four hr after settling, zygotes had developed into spherical bodies, 3.5–4.5 μm diam., surrounded by thin cell walls and containing two chloroplasts and a stigma. The swimming period of planozygotes was shorter than that of uncopulated gametes, which continued to swim ten hr after liberation. Twenty-four hr after liberation, uncopulated gametes followed the pattern of zygotes in settling and becoming spherical on the substratum, but faded away within a few days. No parthenogenetic reproduction was observed.

6. *Germination and development of zygotes*: The spherical bodies did not immediately produce germ tubes, but continued to enlarge for about one month. Five days after settling, the number of chloroplasts

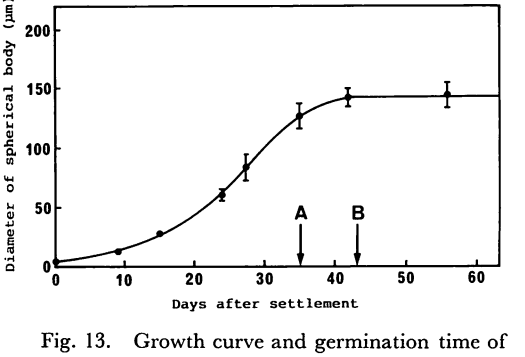
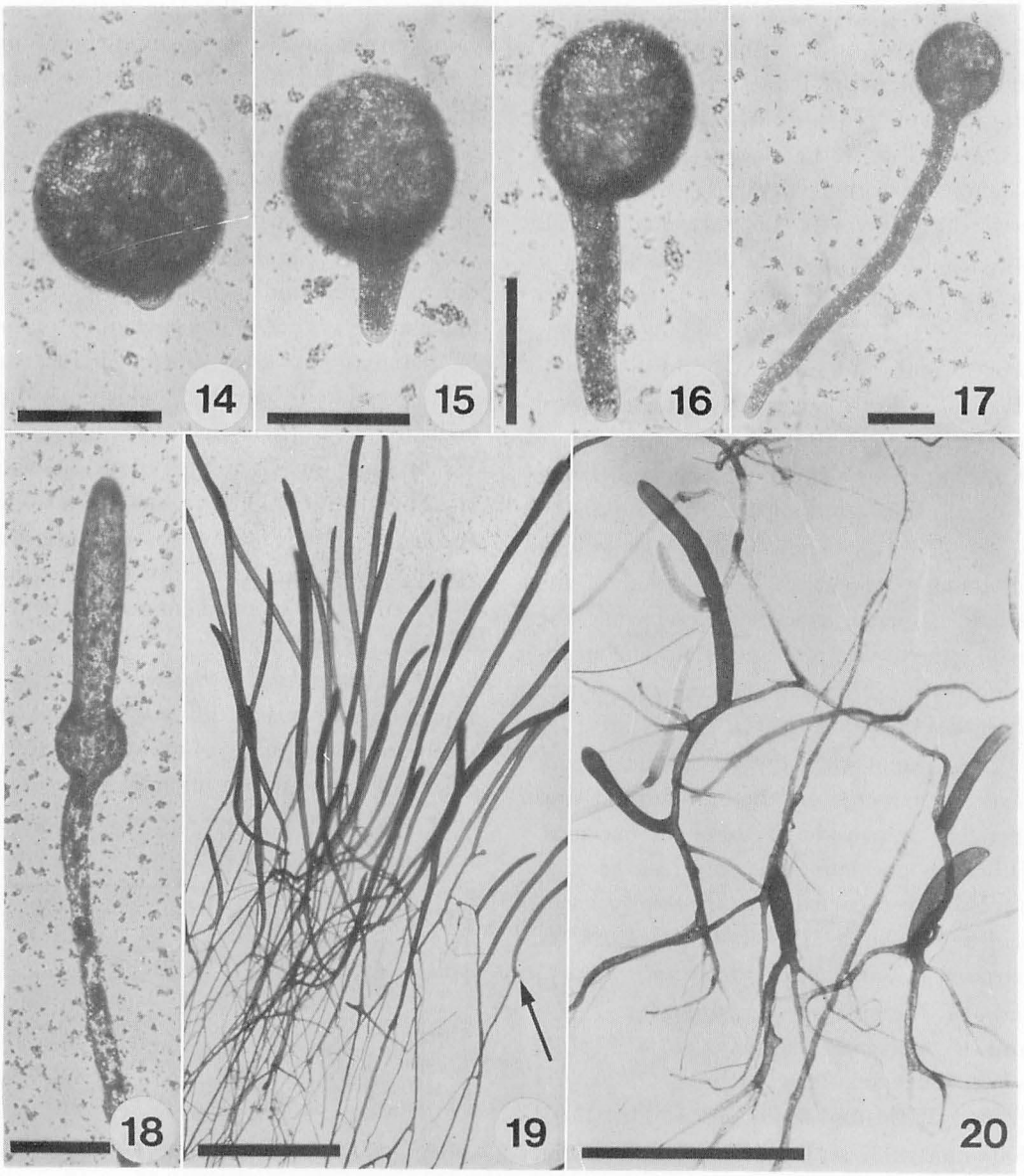


Fig. 13. Growth curve and germination time of spherical bodies of *C. racemosa* var. *laetevirens* under 25.0°C, 3.0 klux, 14L/10D hr cycle. Bars represent standard deviations. A. Beginning of germination. B. Beginning of secondary germ tube formation.

had increased to 3–6, and the stigma had disappeared. After 15 days, the spherical bodies had enlarged further, contained numerous chloroplasts, and appeared to have a distinctive cell wall (Fig. 11). After 24 days, they attained a diameter of 55–65 μm (Fig. 12). The chloroplasts and other organelles were distributed along the entire inner surface of the spherical bodies.

After about 35 days, the spherical bod-



Figs. 14–20. Germination and development of *C. racemosa* var. *laetevirens*. 14. Primary germ tube formation, 35 days after settling. 15. Primary germ tube elongation, after 37 days. 16. After 39 days. 17. After 42 days. 18. Germling with a fine primary germ tube and a thick secondary one, after 47 days. 19. Protonema-like plants with thin and thick filaments, original cell shown with an arrow, after 2 months. 20. Erect shoots from creeping filaments, after 3 months. Scale: (Figs. 14–17) = 100 μm, (Fig. 18) = 200 μm, (Figs. 19, 20) = 5 mm.

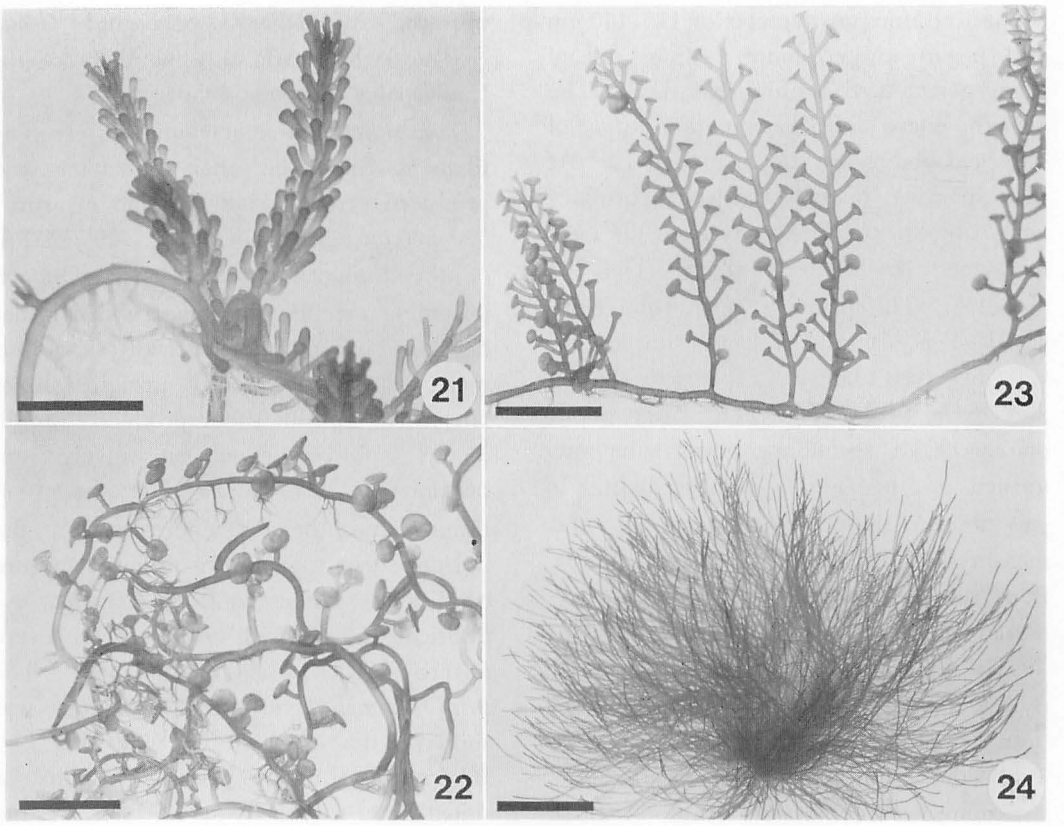
ies had attained a diameter of 115–140 μm and began to germinate. Almost all of them germinated within five days. The growth curve and germination time of spherical bodies are shown in Fig. 13. At first, spherical bodies produced a primary germ tube on the side away from the light measuring 30–40 μm in diam. (Figs. 14 and 15). The primary germ tube elongated (Figs. 16 and 17) and no septum was observed between spherical bodies and germ tubes (Fig. 17). After about one week, a secondary germ tube was formed on the side facing the light. It was thicker than the primary one and measured 90–130 μm in diameter (Fig. 18). Both tubes elongated and branched. About one month after germination, germlings developed into creeping, filamentous, protonema-like plants which consisted of branched thick and thin filaments (Fig. 19). Trabeculae and vigorous protoplasmic streaming were observed inside the thick filaments.

In spite of many culture studies of the spherical stage of *Caulerpa* zygotes, their germination was not reported until recently. In *C. serrulata* (PRICE 1972) and *C. okamurae* (ISHIWARA *et al.* 1981), zygotes germinated bipolarly about seven weeks after settling. The zygotes of the present alga also germinated bipolarly, five weeks after settling. Because the spherical bodies continued to increase their cell volume prior to germination, this period is not considered as dormancy, but as a preparatory step for germ tube formation. In the present alga, a fine primary germ tube was formed on the side away from the light, whereas a thick secondary one was formed on the side facing the light. The developmental sequence, as in the present alga, has not been clarified in other species of *Caulerpa*, but has been observed in *Halimeda tuna* and *Udotea petiolata*, which are also members of the Caulerpales (MEINESZ 1980).

Two months after germination, creeping filaments increased their diameter and produced primary shoots which measured 300–500 μm in diam. (Fig. 20). Most of these shoots continued to elongate, becoming creeping rhizomes which either developed directly into upright shoots or, more usually, produced upright shoots later. An upright shoot produced ramuli at its apical portion successively and became an assimilator. The shapes of ramuli and their arrangement on the upright shoot varied with different culture conditions. Under 20.0°C, 5.0 klux, cylindrical ramuli with obtuse heads were formed in a radial arrangement. The form of well-developed assimilators was similar to that of the mother plant (Fig. 21). By contrast, under 25.0°C, 1.5 klux, a shield-form ramulus was formed at the tip of each erect shoot, the fronds being similar to those of *C. racemosa* var. *peltata* (Fig. 22). Moreover, under 20.0°C, 1.5 klux or 25.0°C, 5.0 klux trumpet-form ramuli were formed alternately on an upright shoot. The well-developed assimilators were not similar to those of the mother plant, but were intermediate between the *laetevirens*-type and the *peltata*-type (Fig. 23).

When zygotes were inoculated in high density, they did not differentiate into thick rhizomes, upright shoots and ramuli, but developed into tufty, sometimes branched, filamentous plants which were similar to *Derbesia* or *Chlorodesmis* (Fig. 24).

PRICE (1972) pointed out that a germling of *C. serrulata* produced a pinnate branch (assimilator) which was very different from the mother plant. ISHIWARA *et al.* (1981), on the other hand, reported that



Figs. 21–24. Plants of *C. racemosa* var. *laetevirens* cultured under different conditions. 21. *Laetevirens*-type plant, cultured under 20.0°C and 5.0 klux, after 6 months. 22. *Peltata*-type plant, cultured under 25.0°C and 1.5 klux, after 6 months. 23. Intermediate-type plant, cultured under 20.0°C and 1.5 klux, after 6 months. 24. Tufty filamentous plant, cultured under 25.0°C and 5.0 klux, after 3 months. Scale: (Figs. 21, 23)=10 mm, (Figs. 22, 24)=20 mm.

the new plants derived from zygotes of *C. okamurae* were similar to the mother plant. In the present alga, germlings derived from the same mother plant produced three types of assimilators according to different culture conditions. It seems that these morphological variations are not caused by genetic polymorphism, but depend on culture conditions. The whole process of assimilator formation and analysis of the morphological variations under various conditions will be detailed in a subsequent article.

7. *Reproduction of cultured plants*: About six months after inoculation, germlings developed into mature plants and became fertile. They produced biflagellate male and female gametes on the same plant, which copulated with each other. The process of gamete formation, gamete liberation, and developmental sequences were similar to those of the mother plant. Quadriflagellate or stephanokontic zooids, which have been reported in the sporophytes of some members of the Bryopsidales (HUSTEDE 1964, RIETEMA 1972, VAN DEN HOEK *et al.* 1972, TATEWAKI 1973, 1977, KOBARA & CHIHARA 1978a, 1978b, 1984, and OKUDA *et al.* 1979), were not observed.

8. *Life history*: In the present alga, the zygotes derived from wild plants developed

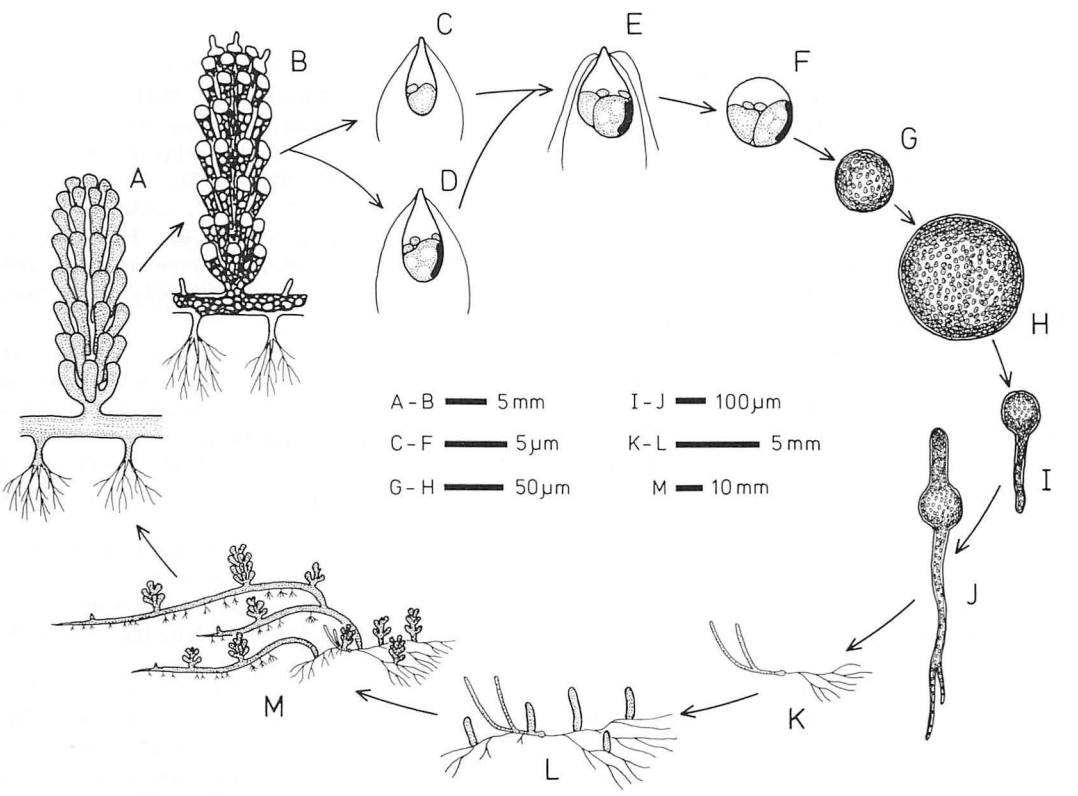


Fig. 25. Life history of *C. racemosa* var. *laetevirens*. A. Vegetative plant. B. Fertile plant with protoplasmic networks. C. Male gamete. D. Female gamete. E. Planozygote. F. Settled zygote. G. Spherical body, 3 weeks after settling. H. Enlarged spherical body, after 5 weeks. I. Germination, germling with a primary germ tube, after 6 weeks. J. Germling with a primary and a secondary germ tube. K. Protonema-like plant. L. Creeping filament with erect shoots. M. Juvenile plant with assimilators.

directly into macroscopic plants which also produced both male and female gametes. The resulting zygotes also developed directly into macroscopic plants. SCHUSSNIG (1939) demonstrated meiosis in gametogenesis of *C. prolifera*. Although the present study lacks cytological observations, a scheme showing the succession of somatic stages in the life history of *C. racemosa* var. *laetevirens* can be drawn (Fig. 25). GOLDSTEIN and MORRALL (1970) suggested the possibility of an alternation of heteromorphic generations in *Caulerpa*, but the present study does not support this idea.

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榎本幸人・大葉英雄*：緑藻スリコギヅタの生殖，発生，体形成について

室戸岬および奄美大島産のスリコギヅタの生殖，発生，体形成を単藻培養により観察した。5～7月に採集した野生体は両産地のものとも25℃，1.0～3.0 klux，14 L/10 D の条件下で1カ月以内に成熟し，同一藻体に2鞭毛の雌雄配偶子を形成する。雌性配偶子は大型で1個の眼点をもち，雄性配偶子は小型で眼点を欠く。雌雄配偶子は接合して接合子となり，基物に定着し球形化する。その後の生育も両産地のものの間で差はなく，球形体は球状のまま肥大生長し，約5週間後に二極的に発芽する。細胞の反光源側に細い第一次発芽管を，次いで光源側に太い第二次発芽管を形成する。発芽管は伸長，分岐し糸状の protonema 様体となり，匍匐茎および直立茎を形成する。直立茎は小枝を形成し直立部に発達する。20℃，5.0 klux の培養条件下で直立部はスリコギヅタ状，25℃，1.5 klux ではタカツキヅタ状，20℃，1.5 klux あるいは25℃，5.0 klux では両者の中間型を示す。4～6ケ月後，藻体は成熟し同一藻体上に2鞭毛の雌雄配偶子を形成する。多鞭毛性の遊走細胞は観察されなかった。(656-24 兵庫県津名郡淡路町　神戸大学理学部臨海実験所。*現住所：108 東京都港区港南4-5-7　東京水産大学植物学教室)