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PRELIMINARY STUDIES ON THE PHOTOSYNTHESIS AND RESPIRATION OF *PORPHYRA YEZOENSIS* UNDER EMERSED CONDITIONS[*1]

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Photosynthesis and dark respiration of *Porphyra yezoensis* thalli under emersed conditions were measured and compared with those under submerged conditions to make clear how and to what degree the photosynthesis and dark respiration occur in air while thalli are emersed. The light-saturated net photosynthetic rate under emersed conditions increased from the start of measurement to reach a maximum and then decreased with water loss. Within the temperature range of 5-30°C, the higher the temperature, the faster the net photosynthesis reached a maximum and the shorter was the period in which the maximum was maintained. This is possibly considered to be correlative with faster desiccation of thalli at higher temperatures. The net photosynthetic rate reached a maximum at water loss of about 16%, began to decline at water loss of about 32%, and reached almost zero when water loss exceeded about 90%. Emersed net photosynthesis was saturated at about 15 klux and 10 and 15°C, while at 20 and 30°C it was not saturated until 30 klux. The light-saturated net photosynthetic rate increased with temperature increase until 25°C, and decreased at 30°C. Emersed dark respiration declined with increase of water loss from thalli. It increased almost linearly with temperature increase in the range of 10-30°C. The light-saturated net photosynthetic rate was about 20% higher under emersed conditions than under submerged ones.

Introduction

The algae growing in the intertidal zone get emersed and submerged, suffering from periodical desiccation. The physiological response of intertidal algae to emersion has been studied in order to explain their vertical distributions. Studying the relationship between photosynthesis and exposure, Stocker and Holdheide (1937) found that the photosynthetic rates of marine algae under exposed conditions on rocky shore were higher than those of submerged algae. In more recent investigations by Bidwell and Craigie (1963), Brown and Johnson (1964), Chapman (1966), Kremer and Schmiz (1973), Quadir *et al.* (1979), and Oates and Murray (1983), however, it is reported that photosynthesis of intertidal algae exposed to atmosphere was either lower than or approximately equal to that under submerged conditions. On the other hand, Johnson *et al.* (1974) found that photosynthesis in air, at constant light and temperature, was considerably greater than that in water with such species as *Iridaea flaccida*, *Porphyra perforata*, *Fucus distichus* and *Endocladia muricata* from the middle or upper intertidal region, while such lower littoral species as *Ulva expansa* and *Prionitis lanceolata* showed reduced photosynthesis in air. Brinkhuis *et al.* (1976) reported that desiccation of

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exposed thalli of *Ascophyllum nodosum* ecad *scorpioides* and *Fucus vesiculosus* had the most pronounced effect on photosynthesis, which increased slightly at water loss from 0 to 25%, then levelled off, and decreased sharply at water loss exceeding 50%.

Being one of the economically important marine algae in Japan and in some other countries, *Porphyra* is cultivated in the floating system as well as in the fixed pole system, and the effect of emersion on photosynthesis and growth of *Porphyra* thalli is one of the most important considerations. In the floating system, *Porphyra* thalli on the Nori net are usually never exposed to air except the period of artificial emersion by emersion control raft for getting rid of attached weed algae. In the fixed pole system, *Porphyra* thalli are exposed to air periodically during low tide.

Early investigations of the effect of emersion on *Porphyra* were reported by Fujikawa (1932, 1937), Kaneko (1940, 1941) and Kurakake (1941). A number of recent works on the effects of emersion (Iwasaki and Matsudaira, 1956; Ogata, 1963; Ogata and Matsui, 1963, 1965; Iwasaki, 1965; Imada *et al.*, 1970; Ogata and Schramm, 1971; Watanabe *et al.*, 1971; Oohusa *et al.*, 1978) dealt with the influence on physiological activity. The effects of emersion on growth and submerged photosynthesis of *Porphyra* thalli, cultured under emersed and submerged conditions over a long period of time, were reported by Ogata and Schramm (1971) and Tajiri and Aruga (1984). Photosynthesis and respiration of *Porphyra* thalli under submerged conditions were reported by Ogata and Matsui (1963) and Nozawa (1967) with *P. tenera*, by Satomi *et al.* (1968), Oohusa *et al.* (1977) and Kato and Aruga (1984) with *P. yezoensis*, and by Ogata and Schramm (1971) with *P. umbilicalis*. However, no investigations so far have been reported on photosynthesis of *Porphyra* thalli under emersed conditions.

In estimating the productivity of intertidal marine algae based upon photosynthesis and in investigating the effects of emersion on growth and photosynthesis in water of *Porphyra*, one must take account not only of photosynthesis in water but also of the photosynthesis that occurs in air under exposed conditions, particularly since it might be probable that the photosynthetic responses of algae to light intensity and temperature or photosynthetic performance in air are different from those in water even under similar conditions of light and temperature.

In the present study it was attempted to determine the photosynthetic responses of *Porphyra yezoensis* in air under different conditions of light and temperature, and the photosynthesis in air was compared with that in water in order to obtain a general knowledge of photosynthesis in air and furthermore to make clear the effects of emersion on photosynthesis and respiration.

Material and Methods

From the stock of free-living conchocelis stage of *Porphyra yezoensis* maintained in the laboratory a cluster of filaments was collected and cultured in an incubator under 10:14 LD cycle at 15°C (light period: 08:00-18:00 at about 14 klux). Illumination was provided by fluorescent lamps (Toshiba, 30 W White). Synthetic fibers (vinylon monofilaments) about 3 cm long were put into the culture. After 6-10 days, conchospores were shed, immediately attached to the synthetic fibers and started to grow into thalli. Zero day was assigned to the age of the thalli on the day of attachment. The thalli were detached from the synthetic fiber at the age of about 20 days old. The culture medium was renewed every other day throughout the culture period, and all cultures were kept aerated. For culture medium the seawater collected from the Kuroshio area off the Izu Oshima Island was filtered with a glass fiber filter (Whatman GF/C) and enriched with PES medium (Provasoli, 1966) after being autoclaved. Salinity and pH of the culture medium were 32-33‰ and 8.4-8.6, respectively. Thalli grown up to about 5 cm long (about 50 days old) were used for the measurements of photosynthesis and respiration.

Sample thalli of *P. yezoensis* cultivated with the fixed pole system and with the floating system in the Nori farm at Shitazu, Futtsu, Chiba Prefecture, were collected on December 19, 1985, transported to the laboratory in Tokyo, and used also for the measurements of photosynthesis and respiration. They were maintained for 3 days under the same conditions as in laboratory cultures before use, during which period the thalli from the fixed pole system were exposed to air one hour daily (11:00-12:00) for two days.

For the measurements of emersed photosynthesis and respiration, samples were carried to Laboratory of Plant Ecology, Faculty of Science, University of Tokyo, which took about an hour. Photosynthesis and respiration of *P. yezoensis* thalli under emersed conditions were measured with a system shown in Fig. 1, which employs an infrared gas analyzer (IRGA, KOKA Electric Factory, IR-21) for determining CO_2 concentration in air. Thalli were placed in a plexiglass assimilation chamber (10×14×2 cm or 11×20×2 cm) maintained in a growth chamber (NKS, LH-200-R). Temperature of the air in the assimilation chamber was controlled indirectly by controlling the temperature in the growth chamber. It was attained with an accuracy of ±0.5°C. Air was supplied with

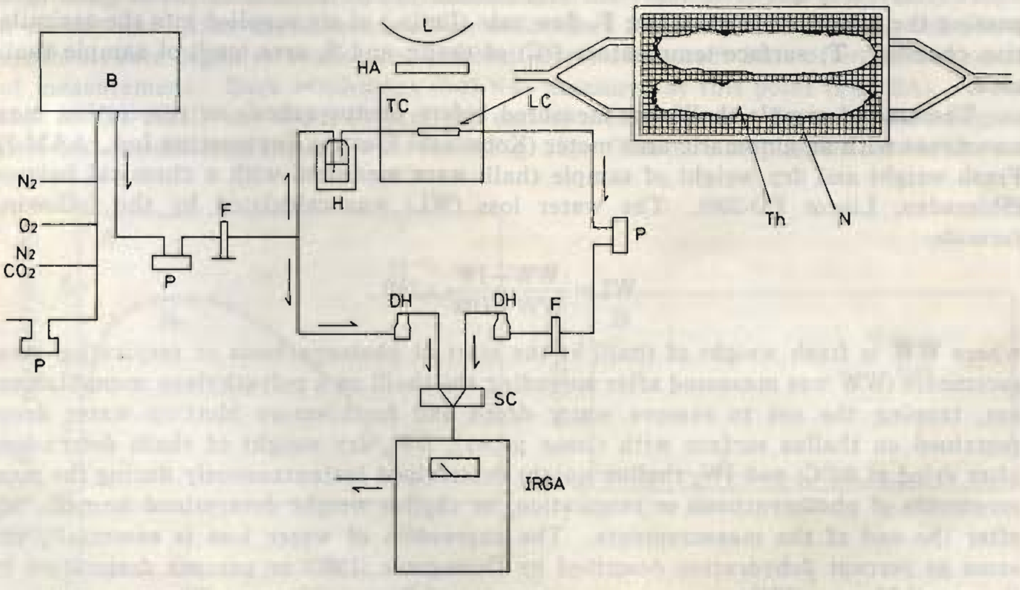

Fig. 1. Outline of the equipment for measuring emersed photosynthesis and respiration. B, air bag; P, pump; F, flow meter; H, humidifying bottle; L, light source; HA, heat-absorbing water filter; TC, temperature-controlling cabinet; LC, assimilation chamber; Th, thallus; N, nylon net; DH, dehydration bottle; SC, changeover switch; IRGA, infrared gas analyzer.

a pump from the air bag to IRGA through the assimilation chamber along the line shown in Fig. 1. The rate of flow was controlled at 2 l/min. with a needle-valve flow meter. The outlet CO_2 concentration, surface temperature of thalli and air temperature in the growth chamber were simultaneously recorded with a high-speed recorder (RDK, R-10H-12S). CO_2 concentration was determined with IRGA. The instrument was calibrated using standard gases. Thalli were spread on a polyethylene monofilament net (18 mesh) and placed in the assimilation chamber. Light was supplied from above with a halogen lamp (Toshiba, 200 V 1000 W) for photosynthesis measurements. A 10 cm thick water filter was placed between the growth chamber and the light source to reduce heat. Light intensity was measured with a photocell illuminometer (Toshiba, SPI-5). The surface temperature of thalli was measured with a temperature sensor located under the thalli.

For photosynthesis-light curves, measurements were carried out at various light intensities which were attained in a stepwise fashion from the highest to the lowest by changing paper filters of varied transmissivity. Temperatures were increased in a stepwise way from the lowest to the highest in the measurements for photosynthesis-temperature curves and respiration-temperature curves. Dark respiration was determined by completely covering the assimilation chamber with opaque plastic.

Photosynthesis (P) or respiration (R) rate ($mgCO_2/dm^2/hr$) was calculated by the following equation:

$$\text{P or R}=\frac{A-B}{10^6}\times F\times\frac{273}{273+T}\times\frac{44}{22.4}\times\frac{100}{S}\,, \times 60$$

where A and B respectively represent CO_2 concentrations (ppm) of air before and after passing the assimilation chamber; F, flow rate (l/min.) of air supplied into the assimilation chamber; T, surface temperature (°C) of thalli; and S, area (cm^2) of sample thalli used.

The area of sample thalli was measured befere photosynthesis or respiration measurements with an automatic area meter (Kobayashi Electric Engineering Inc., AAM-7). Fresh weight and dry weight of sample thalli were measured with a chemical balance (Shimadzu, Libror ED-200). The water loss (WL) was calculated by the following formula:

$$WL=\frac{WW-IW}{WW-DW}\times 100\,,$$

where WW is fresh weight of thalli at the start of photosynthesis or respiration measurements (WW was measured after spreading the thalli on a polyethylene monofilament net, tapping the net to remove water drops and furthermore blotting water drops remained on thallus surface with tissue paper); DW, dry weight of thalli determined after dried at 80°C; and IW, thallus weight determined instantaneously during the measurements of photosynthesis or respiration, or thallus weight determined immediately after the end of the measurements. The expression of water loss is essentially the same as percent dehydration described by Dromgoole (1980) or percent desiccation by Oates and Murray (1983).

Submerged photosynthetic and dark respiration rates were determined by the light and dark bottle method. One or more thalli were placed in a D.O. bottle of about 100 ml filled with filtered seawater, and incubated for 15-30 min. for photosynthesis and one hour for respiration measurements in a water tank. Temperature of water in the water tank was controlled by using a Taiyo Coolnit (CL-30). The oxygen concentration in seawater was determined by the Winkler titration technique before and after incubation. Photosynthesis-light curve was obtained at 15°C at various light intensities by changing the distance of D.O. bottles from the light source. Light intensity was measured with an LMT illuminance meter. A photoreflector lamp (Toshiba, 100 V 500 W, Spot) was used for photosynthesis measurements. The measurements were started in the middle of light period to exclude the effect of diurnal rhythm (Mishkind *et al.*, 1979). The photosynthetic and dark respiration rates under submerged conditions determined by measuring changes of dissolved oxygen were converted from $mgO_2/dm^2/hr$ to $mgCO_2/dm^2/hr$ by taking the photosynthetic quotient as unity to be compared with the photosynthetic and dark respiration rates under emersed conditions.

Some thalli cultured in laboratory under the conditions mentioned above were exposed to air for 1 hr daily (11:00-12:00, light period emersion) for ten days, while other thalli of the same age were simultaneously maintained in seawater. The emersion treatment started when the thalli were about 4 cm long (40 days old). Polyethylene monofilament net was used to scoop up thalli from seawater in a tray and to spread them on it. The net with the thalli on it was placed in the same incubator used for maintaining the cultures.

Results

Examples of the changes of emersed net photosynthesis and respiration rates of *Porphyra yezoensis* thalli are shown in Fig. 2. Net photosynthesis rate was low at the beginning of the measurement, i.e. immediately after emersed, and increased to reach a maximum. After the maximum was maintained for more than 30 min., net photosynthesis rate began to decline and reached nearly zero about 3 hrs after the beginning of measurement. Dark respiration (Rd) was measured at this point (Fig. 2A). Water loss of the thalli was about 79% at the end of measurement. Emersed dark respiration decreased almost linearly with time (Fig. 2B). The dark respiration rate at the end

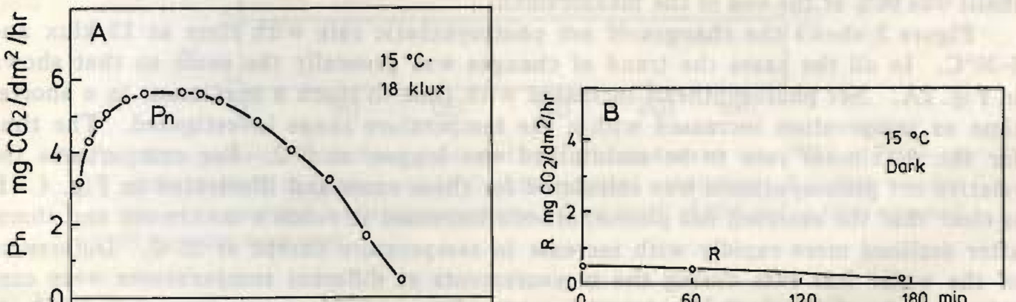

Fig. 2. Changes with time of emersed net photosynthesis at 18 klux (A) and dark respication (B) of *Porphyra yezoensis* thalli at 15°C. Rd shows a dark respiration rate obtained after photosynthesis measurements. (A) A thallus of 34.6 cm² and 44 days old. (B) Five thalli of 85.0 cm² in total area and 54 days old.

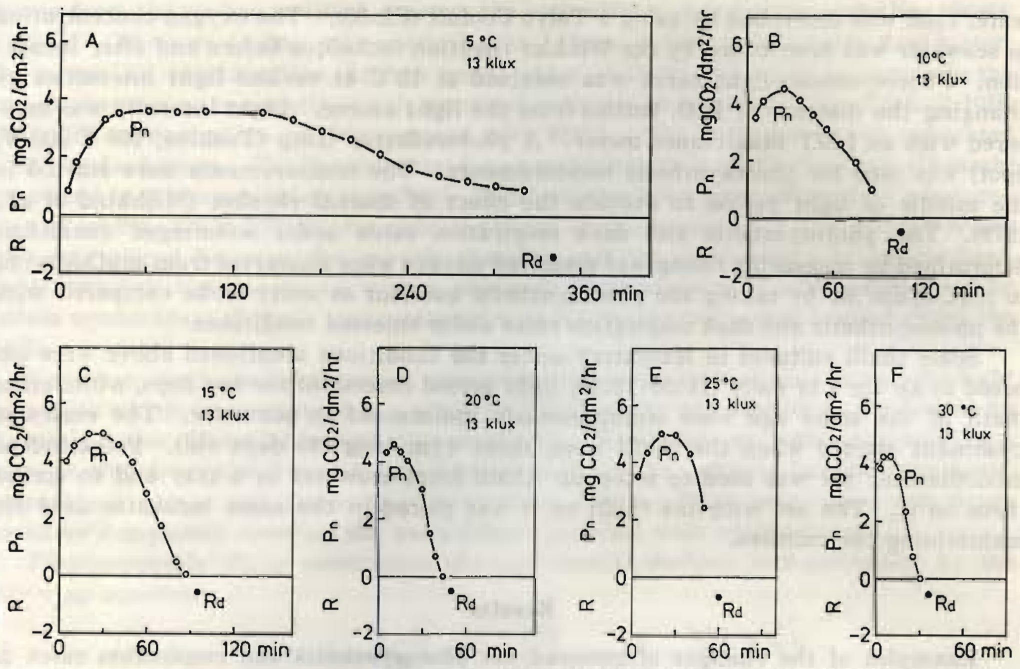

Fig. 3. Changes with time of emersed net photosynthesis (Pn) of *Porphyra yezoensis* thalli at 13 klux and various temperatures of 5-30°C. Rd, a dark respiration rate obtained after photosynthesis measurements at various temperatures. A, a thallus of 38.1 cm^2 and 45 days old; B, a thallus of 29.3 cm^2 and 46 days old; C, a thallus of 25.4 cm^2 and 43 days old; D, a thallus of 20.6 cm^2 and 43 days old; E, a thallus of 39.0 cm^2 and 46 days old; F, a thallus of 25.0 cm^2 and 46 days old.

of measurement was reduced to about 80% of that at the beginning. Water loss of the thalli was 96% at the end of the measurement.

Figure 3 shows the changes of net photosynthetic rate with time at 13 klux and 5-30°C. In all the cases the trend of changes was generally the same as that shown in Fig. 2A. Net photosynthesis increased with time to reach a maximum in a shorter time as temperature increased within the temperature range investigated. The time for the maximum rate to be maintained was longest at 5°C. For comparisons the relative net photosynthesis was calculated for these cases and illustrated in Fig. 4. It is clear that the emersed net photosynthesis increased to reach a maximum and thereafter declined more rapidly with increase in temperature except at 25°C. Differences of the water loss rate during the measurements at different temperatures were considered to be the main factor for the result. The water loss was determined only at the end of these measurements; it was 85-95%. The water loss during the measurement of emersed photosynthesis was determined only at 15°C and 15 klux in another separate measurement. It increased almost linearly with time as shown in Fig. 5. Net photosynthesis increased with time and reached a maximum at water loss of about 16% (40 min. after the start of measurement). The level of net photosynthesis was maintained for more than 40 min. until water loss reached about 32%. Net photosynthesis declined gradually as water loss exceeded 35%.

Fig. 4. Changes with time of relative net photosynthesis of *Porphyra yezoensis* thalli under emersed conditions at 13 klux and 5-30°C. Redrawn from Fig. 3.

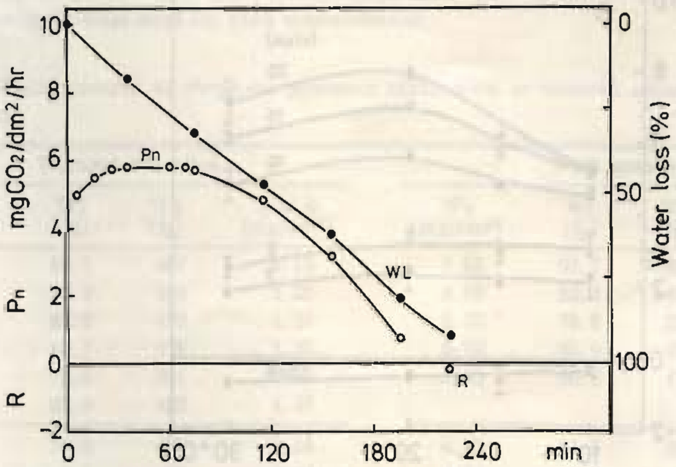

Fig. 5. Changes with time of net photosynthesis (Pn) and water loss (WL) of *Porphyra yezoensis* thalli at 15 klux and 15°C under emersed conditions. R is dark respiration after photosynthesis measurements. Two thalli of 80.6 cm^2 in total area and 65 days old were used.

The photosynthetic responses to light and temperature of thalli while emersed were investigated. Photosynthesis-light curves and photosynthesis-temperature curves are shown in Fig. 6. In the photosynthesis-light curves (Fig. 6A), the net photosynthesis was saturated at 15 klux at 10 and 15°C, while at 20 and 30°C it was not saturated even at 30 klux. In the photosynthesis-temperature curves (Fig. 6B), the net photosynthetic rate changed little with temperature at 3 and 5 klux within the temperature range investigated, while at higher light intensities it increased with temperature to show a maximum at 20-25°C and decreased at higher temperature. The dark respira-

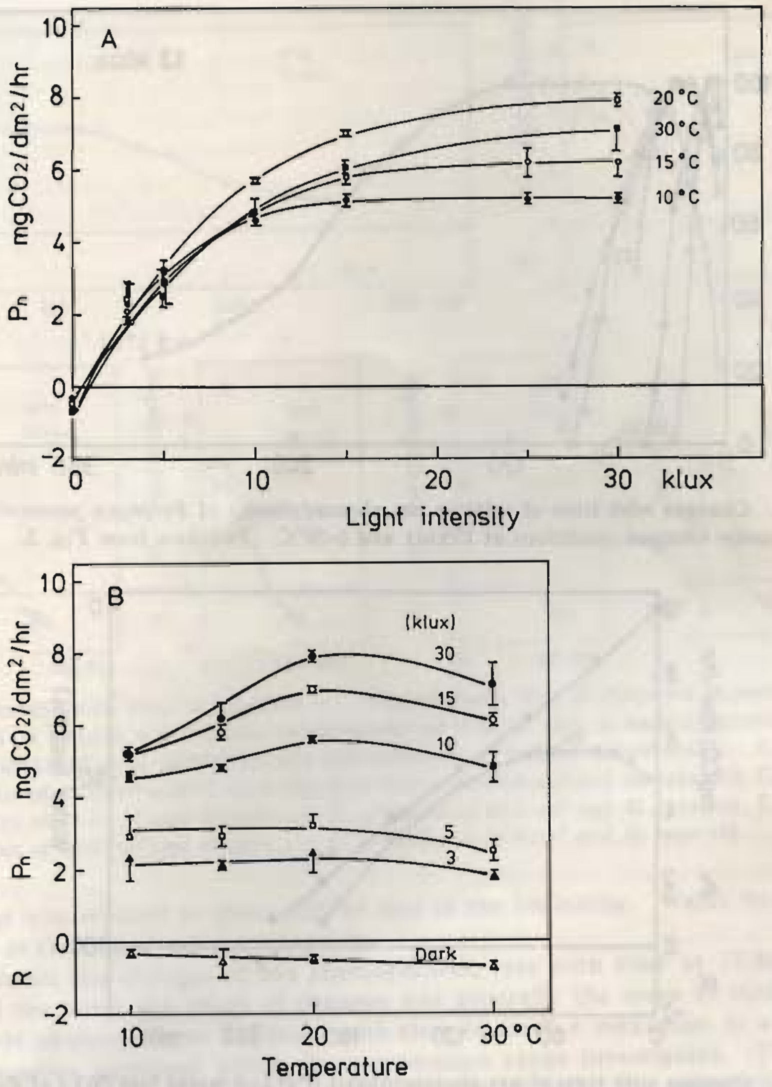

Fig. 6. Photosynthesis-light curves (A), photosynthesis-temperature curves (B) and a respiration-temperature curve (B) of *Porphyra yezoensis* thalli at various light intensities and temperatures under emersed conditions. Each datum represents the mean of ten thalli in two measurements. Vertical bar indicates 95% confidence interval.

tion rate (Fig. 6B) increased linearly with increase in temperature in the range investigated.

Changes of emersed photosynthesis of thalli with periodical emersion treatment (1 hr/day for 10 days) were compared with those of thalli without emersion treatment (Fig. 7). The emersed net photosynthetic rate of thalli with emersion treatment increased to reach a maximum slightly earlier and lasted longer than that of thalli

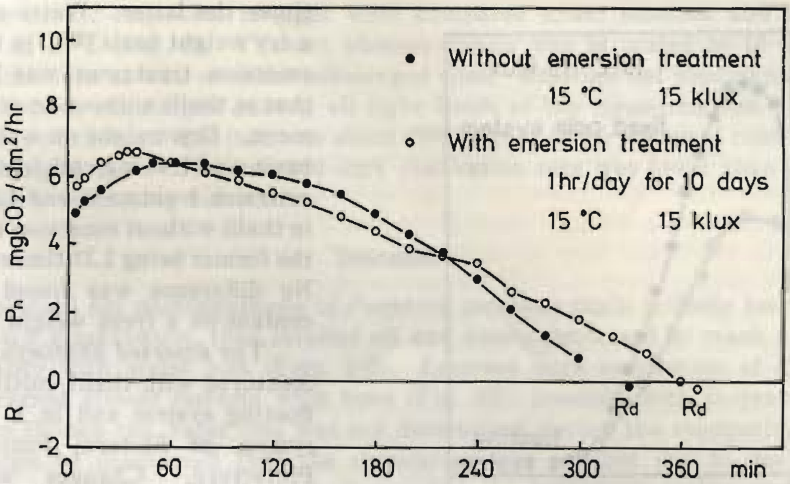

Fig. 7. Changes with time of emersed net photosynthesis of *Porphyra yezoensis* thalli with or without emersion treatments during laboratory culture. Measured at 15 klux and 15°C. Rd is dark respiration after photosynthesis measurements. Three thalli were used for each measurement.

Table 1. Water content of *Porphyra yezoensis* thalli with or without emersion treatments.

	Without emersion				With emersion			
	Ws (mg/cm^2)	Wf (%)	Wd (%)	d.w./s (mg/cm^2)	Ws (mg/cm^2)	Wf (%)	Wd (%)	d.w./s (mg/cm^2)
	5.24	80.3	407	1.15	5.62	97.7	393	1.42
	4.68	79.5	389	1.20	6.68	82.4	469	1.45
	5.23	82.0	456	1.29	5.32	78.8	372	1.43
	4.81	80.7	418	1.15	8.70	85.9	609	1.44
	3.23	73.8	281	1.13	5.93	80.6	415	1.41
	5.51	82.8	480	1.17				
$\bar{X}$	4.78	79.9	405	1.18	6.45	81.5	452	1.43
SD	0.82	3.2	69	0.06	1.36	2.8	95	0.02

Ws, water content on a thallus area basis; Wf, water content on a fresh weight basis; Wd, water content on a dry weight basis; d.w./s, dry weight on a thallus area basis.

without emersion treatment. The emersed dark respiration rate measured when emersed net photosynthesis approached to zero was seemingly higher in thalli with emersion treatment than in thalli without emersion treatment. Comparisons of thalli with or without emersion treatments are summarized in Table 1. Clear differences can be seen in water content of thalli both on a thallus area basis and on a dry weight basis, and also in dry weight on a thallus area basis. Water content (Ws and Wd) and dry weight were higher in thalli with emersion treatment than thalli without emersion treatment. Water content on a thallus area basis (Ws) was 6.45 mg/cm^2 in thalli with emersion treatment and 4.78 mg/cm^2 in thalli without emersion treatment, the former being 1.35

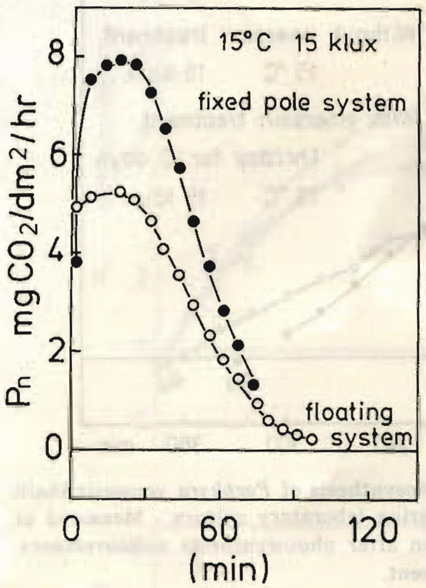

Fig. 8. Changes with time of emersed net photosynthesis at 15 klux and 15°C of *Porphyra yezoensis* thalli cultivated in fixed pole system (●) or in floating system (○) at Shitazu, Futtsu, Chiba Prefecture. Five thalli were used in each measurement.

times the latter. Water content on a dry weight basis (Wd) in thalli with emersion treatment was 1.12 times that in thalli without emersion treatment. Dry weight on a thallus area basis was 1.43 mg/cm^2 in thalli with emersion treatment and 1.18 mg/cm^2 in thalli without emersion treatment, the former being 1.21 times the latter. No difference was found in water content on a fresh weight basis.

The emersed photosynthesis was measured with thalli cultivated in a floating system and in a fixed pole system at Shitazu, Futtsu, Chiba Prefecture. Changes with time of emersed net photosynthesis of these thalli are shown in Fig. 8. Patterns of the changes with time were essentially the same as those obtained with thalli cultured in laboratory. The maximum of emersed net photosynthetic rate was higher in thalli cultivated in a fixed pole system with periodical emersion than in thalli cultivated in a floating system.

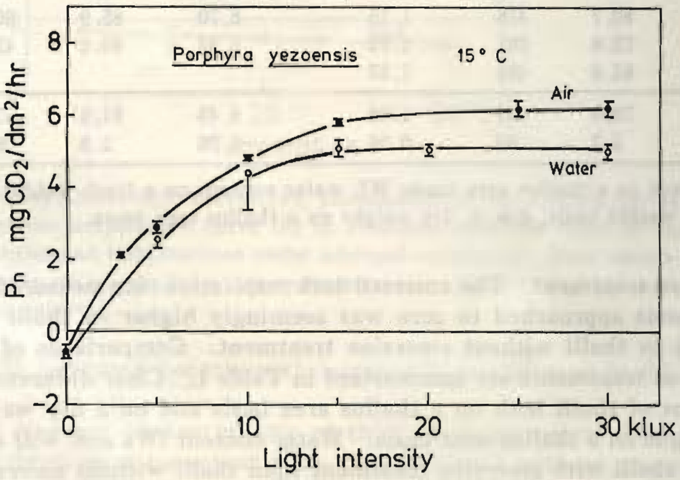

Fig. 9. Photosynthesis-light curves of *Porphyra yezoensis* thalli at 15°C under emersed or submerged conditions.

Photosynthetic responses to light were compared under emersed and submerged conditions at 15°C (Fig. 9). The net photosynthesis was saturated at 15 klux under emersed conditions as well as under submerged ones. Emersed net photosynthetic rates were higher than submerged ones at all light levels of the measurements. The light-saturated net photosynthetic rate was about 20% higher under emersed conditions than under submerged ones. The emersed dark respiration rate was lower than submerged one, but there was no big difference.

Discussion

The emersed net photosynthesis of *Porphyra yezoensis* thalli initially increased with time to reach a maximum, then levelled off and finally decreased to reach almost zero in accordance with water loss (Figs. 2-5). Emersed dark respiration of *P. yezoensis* thalli decreased almost linearly with time (Fig. 2B), possibly with increase of water loss. Even though the water loss was not determined during the respiration measurement, it can be considered that the respiration was reduced due to desiccation of thalli. The emersed net photosynthesis reached the maximum earlier and remained shorter at higher level as temperature became higher within the range investigated except that at 25°C (Figs. 3 and 4). These differences of the change of emersed net photosynthesis with time might be dependent on water loss of thalli during photosynthesis measurements, because the water loss usually proceeds faster at higher temperatures. An exceptional case at 25°C might be related to the difference of area of the thallus used in the measurement, making water loss from a large thallus slower as compared with a small thallus. Maintenance for a long period of a high level of net photosynthetic rate at 5°C seems strange as compared with the results at 10-30°C (Figs. 3 and 4). Further experiments are needed to make sure whether the water loss from thallus is dependent on the thallus area and consequently influences emersed net photosynthesis at various temperatures. The water loss was determined only at 15 klux and 15°C in an assimilation chamber in the present study (Fig. 5). Further experiments are also needed to make sure whether water loss from thallus in light is different from that in the dark.

A relationship of relative net photosynthesis to water loss of thalli is illustrated in Fig. 10. The net photosynthetic rate increased to reach a maximum at water loss of 16%, then levelled off, and began to decline when the water loss exceeded 35%. The initial increase of photosynthesis with increased water loss may be related to the water loss from the surface of thalli as the initial phase of desiccation, thereby possibly enhancing the gas exchange through

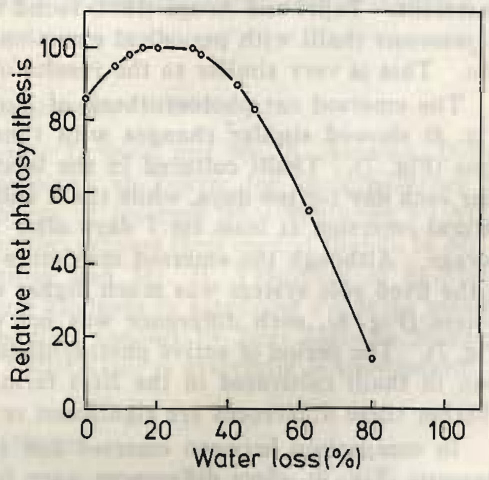

Fig. 10. Relationship between the emersed net photosynthesis and the water loss in *Porphyra yezoensis* thalli at 15 klux and 15°C under emersed conditions.

thallus surface. The decreased photosynthetic rate at a later stage might be caused by the stress due to water loss from thallus cells. Brinkhuis *et al.* (1976) reported with *Ascophyllum nodosum* that photosynthesis in air increased slightly at water loss between 0 and 25%, levelled off and decreased sharply at water loss greater than 50%, while the respiration in air decreased with water loss. Quadir *et al.* (1979) found that the net photosynthesis of *Fucus distichus* reached a maximum at 20% desiccation due to rapidly increasing gross photosynthetic rate and a slowly decreasing respiration. This is similar to the results obtained with *P. yezoensis* in the present study. Brinkhuis *et al.* (1976) reported that the water loss of *A. nodosum* in the assimilation chamber proceeded linearly with time at 13 and 27°C. A similar trend of water loss was observed with *P. yezoensis* at 15°C in the present study. Although water loss curves at different temperatures may have different form, it is reasonable that water loss of *P. yezoensis* thalli proceeded gradually faster as temperature increased from 5 to 30°C, resulting in the changes of photosynthesis within a shorter time (Fig. 4).

The emersed net photosynthesis of *P. yezoensis* thalli with periodical emersion treatment was different from that of thalli without emersion treatment (Fig. 7). The thalli with periodical emersion treatment showed a maximum earlier than did the thalli without emersion treatment. The photosynthetic activity remained longer in the former thalli than in the latter. The emersed respiration rate measured when the net photosynthesis approached zero was a little higher in the thalli with emersion treatment than in the thalli without emersion treatment. Further experiments are, however, necessary to assure whether the differences are significant or not. It is postulated that under emersed conditions the dark respiration or water loss over time in thalli with periodical emersion treatment is different from that in thalli without emersion treatment. The water content and dry weight on a thallus area basis were higher in thalli with periodical emersion treatment than in thalli without emersion treatment (Table 1). Further investigations are needed to confirm whether the difference is related to the difference in emersed photosynthesis of thalli with or without emersion treatment. Tajiri and Aruga (1984) found that the dry weight per unit thallus area of *P. yezoensis* thalli with periodical emersion was 1.3 times that of thalli without emersion. This is very similar to the results obtained in the present measurement.

The emersed net photosynthesis of *P. yezoensis* thalli cultivated in the Nori farm (Fig. 8) showed similar changes with time as those cultured under laboratory conditions (Fig. 7). Thalli cultured in the laboratory were given emersion treatment of 1 hour each day for ten days, while thalli cultivated in the fixed pole system experienced natural emersion at least for 7 days after they were delivered in the sea from frozen storage. Although the emersed maximum net photosynthetic rate of thalli cultivated in the fixed pole system was much higher than that of thalli cultivated in the floating system (Fig. 8), such difference was not observed with thalli cultured in laboratory (Fig. 7). The period of active photosynthesis was longer in thalli cultured in laboratory than in thalli cultivated in the Nori farm. Further investigations are needed to see whether these differences are significant or not.

In comparison between emersed and submerged photosynthesis-light curves of *P. yezoensis* (Fig. 9), clear differences were found in the initial slopes as well as in the light-saturated rates of photosynthesis. The initial slope of the photosynthesis-light curve was steeper in air than in water. The light-saturated rate of net photosynthesis was higher in air than in water.

Johnson *et al.* (1974) reported that photosynthetic rate of *Porphyra perforata* can be 2.84 times greater in air than in water. This value is more than 2 times greater than that (1.22) for *P. yezoensis* cultured in laboratory in the present study: the light-saturated net photosynthesic rate was 5.00±0.15 $mgCO_2/dm^2/hr$ in water and 6.10±0.18 $mgCO_2/dm^2/hr$ in air. The net photosynthetic rate of *P. perforata* reported by Johnson *et al.* (1974) was 9.4±0.5 $mgCO_2/dm^2/hr$ in air and 3.3±0.57 $mgCO_2/dm^2/hr$ in water, with the former greater and with the latter lower than those of *P. yezoensis* cultured in laboratory in the present study. On the other hand, the net photosynthetic rate at 15 klux and 15°C of *P. yezoensis* cultivated in the fixed pole system in the Nori farm was 7.90 $mgCO_2/dm^2/hr$ (one measurement) in air and 3.81±0.50 $mgCO_2/dm^2/hr$ (three measurements) in water, with the former 2.07 times greater than the latter. This value is similar to that of natural *P. perforata* reported by Johnson *et al.* (1974).

It is possible that *P. yezoensis* thalli showed a considerably high activity of photosynthesis while emersed as far as water loss did not exceed 40%. However, the growth of *P. yezoensis* thalli with periodical emersion treatment was reported to be much lower than that of thalli without emersion (Imada *et al.*, 1970; Ogata and Schramm, 1971; Tajiri and Aruga, 1984). Tajiri and Aruga (1984) found that after 3 weeks of emersion treatment the length of thalli with 3 hour emersion per day was 0.7-0.8 times that of thalli without emersion, and that photosynthetic rate under submerged conditions was higher in thalli with emersion treatment than in thalli without emersion. They suggested that the difference in growth might be attributed to the lack of nutrients when thalli were exposed to air. The results of the present study can partly support this suggestion provided that water loss does not exceed the level at which photosyntesis begins to decrease while emersed.

It is clear that the photosynthesis is performed to a considerable extent even under emersed conditions in *P. yezoensis*. The period of exposure to air encountered by such an intertidal seaweed as *P. yezoensis* can not necessarily be regarded strictly as the period of extreme physical stress which is simply tolerated. For *P. yezoensis* the emersed period during which a considerably high photosynthetic rate is observed can be a time of active primary production.

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References

Bidwell, R. J. S. and J. S. Craigie. 1963. A note on the greatly reduced ability of *Fucus vesiculosus* to absorb or evolve CO_2 when not submerged. Can. J. Bot., 41: 171-182.

Brinkhuis, B. G., N. R. Tempel and R. F. Jones. 1976. Photosynthesis and respiration of exposed salt-marsh fucoids. Mar. Biol., 34: 349-359.

Brown, J. M. A. and A. Johnson: 1964. Preliminary studies on the ecology and physiology of *Scytochamus australis* (J. Agardh) HK. et Harv. 1845. Bot. Mar., 6: 233-246.

Chapman, V. J. 1966. The physiological ecology of some New Zealand seaweeds. Proc. Int. Seaweed Symp., 5: 29-54.

Dromgoole, F. I. 1980. Desiccation resistance of intertidal and subtidal algae. Bot. Mar., 23: 149-159.

Fujikawa, K. 1932. [The studies on physiology of *Porphyra* in Korea III.] Annu. Rep. Government General Korean Fish. Res. Lab. 1930. p. 32-125. (in Japanese)

Fujiwara, K. 1937. [The studies on physiology of *Porphyra* in Korea V.] Annu. Rep. Government General Korean Fish. Res. Lab., 8: 1-131. (in Japanese)

Imada, O., Y. Saito and S. Maeki. 1970. Relationships between the growth of *Porphyra tenera* and its culturing condition in the sea II. Influence of atmospheric exposure on photosynthesis, growth and others of *Porphyra* frond. Bull. Jap. Soc. Sci. Fish., 36: 369-376. (in Japanese)

Iwasaki, H. 1965. Studies on the physiology and ecology of *Porphyra tenera*. J. Fac. Fish. Anim. Husb., Hiroshima Univ., 6: 133-211. (in Japanese with Eng. summary)

Iwasaki, H. and C. Matsudaira. 1956. Studies on the physiology of a laver, *Porphyra tenera* Kjellm. Tohoku J. Agric. Res., 7: 65-83.

Johnson, W. S., A. Gigon, S. L. Gulmon and H. A. Mooney. 1974. Comparative photosynthetic capacities of intertidal algae under exposed and submerged conditions. Ecology, 55: 450-453.

Kaneko, M. 1940. [Effect of Hibi emersion on Nori cultivation under light or dark conditions.] Bull. Zenranando Fish. Exp. Sta., 13: 1-28. (in Japanese)

Kaneko, M. 1941. [Effect of Hibi emersion on Nori cultivation under light or dark conditions II.] Bull. Zenranando Fish. Exp. Sta., 14: 1-26. (in Japanese)

Kato, M. and Y. Aruga 1984. Comparative studies on the growth and photosynthesis of the pigmentation mutants of *Porphyra yezoensis* in laboratory culture. Jap. J. Phycol., 32: 333-347.

Kremer, B. P. und K. Schmiz. 1973. CO_2-Fixierung and Stofftransport in benthischen marine Algen. IV. Zur ^{14}C-Assimilation einiger litoraler Braunalgen im submersen und emersen Zustand. Z. Pflanzenphysiol., 68: 357-363.

Kurakake, T. 1941. [Emersion of Nori and uptake of nitrate and nitrite.] Bull. Zenranando Fish. Exp. Sta., 14: 72-80. (in Japanese)

Mishkind, M., D. Mauzerall and S. I. Beale. 1979. Diurnal variation *in situ* of photosynthetic capacity in *Ulva* is caused by a dark reaction. Plant Physiol., 64: 896-899.

Nozawa, K. 1967. On the application of ^{14}C technique to the photosynthesis determination of *Porphyra*. Inform. Bull. Planktol. Japan, Commem. No. Dr. Y. Matsue, p. 175-181. (in Japanese with Eng. abstract)

Oates, B. R. and S. N. Murray. 1983. Photosynthesis, dark respiration and desiccation resistance of the intertidal seaweeds *Hesperophycus harveyanus* and *Pelvetia fastigiata* f. *gracilis*. J. Phycol., 19: 371-380.

Ogata, E. 1963. Manometric studies on the respiration of a marine alga, *Porphyra tenera*—I. Influence of salt concentration, temperature, drying and other factors. Bull. Jap. Soc. Sci. Fish., 29: 139-145. (in Japanese with Eng. abstract)

Ogata, E. and T. Matsui. 1963. Manometric studies on the respiration of a marine alga, *Porphyra tenera*—II. Influence of some growth substances, nitrogen compounds and reappraisal of the influence by drying and pH. Bull. Jap. Soc. Sci. Fish., 29: 991-995 (in Japanese with Eng. abstract)

Ogata, E. and T. Matsui. 1965. Photosynthesis in several marine plants of Japan as affected by salinity, drying and pH, with attention to their growth habitats. Bot. Mar. 8: 199-217.

Ogata, E. and W. Schramm. 1971. Some observations on the influence of salinity on growth and photosynthesis in *Porphyra umbilicalis*. Mar. Biol., 10: 70-76.

Oohusa, T., S. Araki, T. Sakurai and M. Saitoh. 1977. Physiological studies on diurnal biological rhythms of *Porphyra*—I. The cell size, the physiological activity and the content of photosynthetic pigments in the thallus cultured in the laboratory. Bull. Jap. Soc. Sci. Fish., 43:

245-249. (in Japanese with Eng. abstract)

Oohusa, T., S. Araki, T. Sakurai, M. Saitoh, M. Kirita and T. Yamasita. 1978. The diurnal variations in the cell size, in the physiological activity and in the contents of some cellular compounds of *Porphyra yezoensis* f. *narawaensis* in cultivation ground. Bull. Jap. Soc. Sci. Fish., 44: 299-303. (in Japanese with Eng. abstract)

Provasoli, L. 1966. Media and prospects for the cultivation of marine algae. p. 63-75. In: A. Watanabe and A. Hattori (ed.), Cultures and Collections of Algae. Proc. U.S.-Japan Conf. Hakone, Sept. 1966. Jap. Soc. Plant Physiol.

Quadir, A., P. J. Harrison and R. E. DeWreede. 1979. The effects of emergence and submergence on the photosynthesis and respiration of marine macrophytes. Phycologia, 18: 83-88.

Satomi, M., Y. Aruga and K. Iwamoto. 1968. Effect of aging on the seasonal change in photosynthetic activity of *Porphyra yezoensis* grown in the culture ground. Bull. Jap. Soc. Sci. Fish., 34: 17-22.

Stocker, O. und W. Holdheide. 1937. Die Assimilation Helgoländer Gezeitenalgen während der Ebbezeit. Z. Bot., 32: 1-59.

Tajiri, S. and Y. Aruga. 1984. Effect of emersion on the growth and photosynthesis of the *Porphyra yezoensis* thallus. Jap. J. Phycol., 32: 134-146.

Watanabe, T., S. Kato, K. Abe and K. Suzuki. 1971. Studies on the "Shirogusare" disease of "Nori" in Miyagi Prefecture—II. On the exposing effect for the physiology of "Nori" frond. Bull. Miyagi Pref. Fish. Exp. Sta., 5: 13-26. (in Japanese)

スサビノリの干出時の光合成と呼吸に関する研究

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海藻の干出時の光合成及び呼吸がどのように行われているかを明らかにするためスサビノリ (*Porphyra yezoensis*) を用いて予備的な測定を行った。空気中での光合成と呼吸は赤外線ガス分析計により，水中での光合成と呼吸はウィンクラー法により，種々の光及び温度条件のもとで測定した。これらの測定と共に，葉状体の湿重量，乾重量を測定し，water loss (WL) を求めた。

スサビノリの空気中に出た時の光飽和純光合成速度は，初めは WL の増加と共に高まって最大値に達し，その後は WL の増加に伴って低下した。5-30°C の範囲では，温度が高いほど光飽和純光合成速度が最大値に達するのが早かった。これは，温度が高いほど葉状体の乾燥が速く進むことによるものと考えられる。最大値に達した時の WL は約16% で，WL が約32% を越えると純光合成速度は低下し始め，WL がおよそ90%を越えると純光合成速度はほぼゼロになった。空気中の純光合成速度は，10°C と 15°C では約 15 klx で光飽和に達し，20°C と 30°C では約 30 klx でほぼ光飽和に達した。光飽和純光合成速度は，25°C までは温度の上昇に伴って高まったが，30°C では低下した。空気中の呼吸速度は，10-30°C の範囲では温度の上昇に伴ってほぼ直線的に高まり，また，WL の増加に伴って低下した。空気中での光飽和純光合成速度は，水中の場合より約 20% 高かった。スサビノリは WL が約 60% 以下であれば空気中でもかなり光合成を行うことが明らかになった。定期的な干出が光合成や呼吸に及ぼす影響を明らかにするためには，さらに研究を進めることが必要である。