Respiration of Some Marine Plants as Affected by Dehydration and Rehydration*

By

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The marine plants living in the intertidal zone are more or less exposed to air when the water recedes at the ebb. The species inhabiting in the upper part of intertidal zone may be drastically dehydrated whereas the others in the lower part may be slightly dehydrated. Tolerance of such plants to dehydration at the ebb was extensively described by BIEBL (1962) from his "protoplasmatic-ecologic" point of view. Inspite of extensive observations concerning the tolerance of marine plant bodies to dehydration, rather little has been known about the gas metabolism under such dehydrated conditions. Among the few who were interested in such an event, BIDWELL and CRAIGIE (1963) were the first to investigate this problem from the both side of photosynthesis and respiration by using $^{14}CO_2$. They found that *Fucus vesiculosus*, under exposed condition, fixed or evolved CO_2 at a much reduced rate even when its surface was wet and the surrounding atmosphere was in saturated humidity.

OGATA (1963) and OGATA and MATSUI (1963) also investigated the respiration of *Porphyra* when not submerged by manometry. The natural atmosphere surrounding the exposed marine plants is not always humidity-saturated, and the plants are often dehydrated in parched state.

In order to elucidate the respiration of marine plants when they are dried-up into varied degree of dehydration, the present work designed to study the respiration when more than 10 species of the marine plants, some marine phanerogam, and some fresh water phanerogams were exposed with special attention to the comparative physiological tolerance to drying.

Materials and methods

Experiments were carried out in 1964. Fresh plant materials were collected from their natural habitats in the coastal region near the laboratory in Shimonoseki. These materials, with their attributes, are enumerated in Table 1.

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Dehydration was given as follows : the plant body cut into several pieces was blotted quickly ; placed in the tightly closed dessicators containing sulfuric acid of various concentration at the bottom ; and kept there for short period (2～4 hours) or a prolonged (20～24 hours). Dehydration treatments were given under six different conditions, namely, in combinations of three different levels of relative humidity and two different length of time. The plant kept immersed throughout was taken as the control. Seven samples including the control, therefore, for each plant species were subjected to manometric measurement. Measurement was also carried out after "rehydration", namely, returning to the normally immersed condition of the plant material. This treatment provided significant observations as to be described later.

In order to start the manometric measurements at the same time with the materials subjected to different durations of dehydration, the dehydrating treatments were begun at different times to make their end time exactly simultaneous. In practice, the material for prolonged dehydration (20～24 hours) was prepared more earier than that for short dehydration (2～4 hours).

Table 1. Species, phylum, bath-temperature, fresh weight, and date of experiments of materials.

No.	Date		Species	Phylum	Bath-temperature (°C)	Fresh weight (mg)
1	July	1	*Ulva pertusa*	Chlorophyta	25	100
2	〃	8	*Enteromorpha linza*	〃	〃	〃
3	〃	10	*Sargassum thunbergii*	Phaeophyta	〃	300
4	〃	11	*Ishige okamurai*	〃	〃	〃
5	〃	22	*Gelidium amansii*	Rhodophyta	〃	200
6	〃	1	*Gracilaria verrucosa*	〃	〃	300
7	June	30	*Gloiopeltis tenax*	〃	〃	〃
8	July	8	*Laurencia okamurai*	〃	〃	〃
9	〃	4	*Zostera marina*	Marine phanerogam	〃	〃
10	〃	2	*Zostera nana*	〃	〃	〃
11	〃	23	*Potamogeton crispus*	Fresh water phanerogam	27	200
12	〃	24	*Ceratophyllum demersum*	〃	〃	〃

Degree of dehydration was expressed as percentage loss of water, namely, 0 (zero) % at the raw, fresh, blotted condition, and 100 % at the entire loss, respectively. Degree of dehydration expressed by negative value meant the case that the plant body absorbed the surrounding moisture.

Procedure for the measurements under exposed condition was as the following : dehydrating the material as described above ; placing the dried material with no pouring of sea water in the reaction flasks without any aqueous phase ; measuring the rate of respiration with routine method under the respective conditions (Table 1), that is, measuring the oxygen consumption for 1 hour in the dark after 10 minutes of pre-shaking.

Next, the recovery or decrease of respiration of samples were measured after pouring the sea water into reaction flasks. Tolerance to dehydration could be, therefore, estimated by comparing the results obtained under dehydrated and rehydrated states.

Results

Ulva pertusa : Experimental conditions for *Ulva* are presented in Table 2. In the case of saturated (100 %) relative humidity, algal body which had been dehydrated for 3 hours absorbed the moisture and consequently increased in the weight. Such an increase of algal weight due to absorbed moisture was similarly observed more or less in other species. In this case respiration was slightly enhanced over the control case.

Table 2. Experimental conditions for *Ulva pertusa*. Relative humidity (%), duration of desiccation (hr.) and subsequent degree of dehydration (%) under such conditions are shown. Control shows the case when not emerged. Negative value of dehydration indicates the absorption of moisture by plant body.

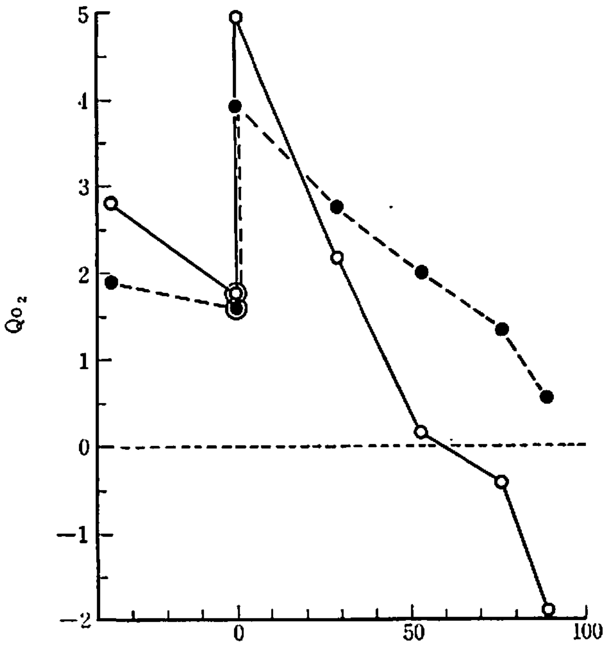
Relative humidity	100	Control	100	75	50	75	50
Duration of desiccation	3	0	20	3	3	20	20
Degree of dehydration	−35.7	0	0	28.6	52.6	75.9	88.6

The dehydration for 20 hours under 100 % r.h. (abbreviation for relative humidity) considerably enhanced the respiration rate even when there was no change in the algal weight. But the respiration was gradually reduced when the dehydration proceeded down to 28.6 and 52.6 %.

It was much interesting but intriguing observation that some sort of unidentified gas evolved under the more intensive dehydration such as 75.9 and 88.6 %. All these facts are presented with the open circles in Fig. 1.

Pouring of sea water into reaction flasks more or less caused the recovery of respiration. The recovery in *Ulva* was only little as shown by the closed circles in Fig. 1. This plant was, therefore, regarded to be weak in the tolerance to dehydration.

Enteromorpha linza : Fig. 2 shows the case of *Enteromorpha*. Slight dehydration as 14.1 % raised the respiration rate, and stronger dehydration reduced the rate as well as in *Ulva* shown in Fig. 1. Excessive dehydration also gave rise to an unidentified gas as well. In this case, the plant body did not show any absorption of moisture even at 100 % r. h., and was observed showing almost remained at the same value of Q_{O_2} as that of control.



Degree of dehydration (%)

Fig. 1. Respiration rate in *Ulva pertusa* under the dehydration and after the rehydration. Open circles : dehydrated state, closed circles : rehydrated state, double circles : control (aqueous phase).

Table 3. Experimental condition for *Enteromorpha linza*. See Table 2 for further legends.

Relative humidity	100	Control	100	75	75	50	50
Duration of desiccation	4	0	23	4	23	23	4
Degree of dehydration	0	0	14.1	68.5	80	93.5	94.2

Recovery of respiration rate caused by rehydration was remarkably observed as indicated by the closed circles in Fig. 2. This species appears to have better tolerance to prior dehydration than *Ulva*. Slight output of unidentified gas was observed at 94.2 % dehydration. Experimental conditions for *Enteromorpha* is presented in Table 3.

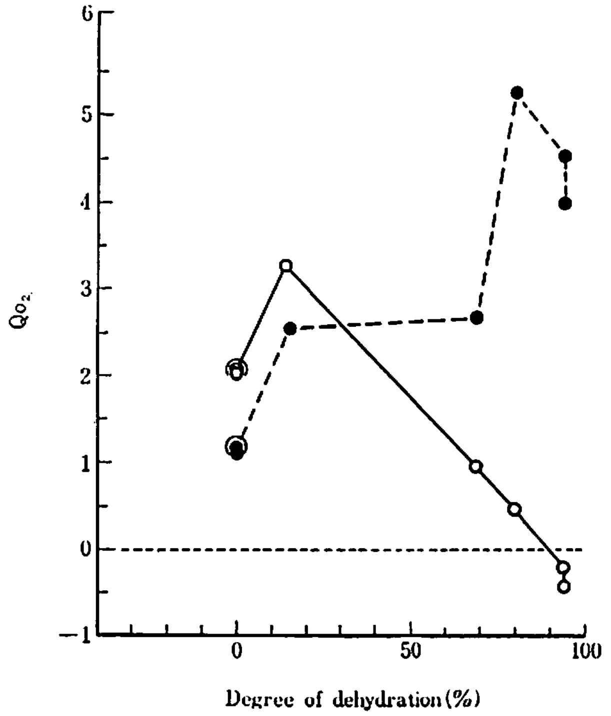


Fig. 2. Respiration rate in *Enteromorpha linza* under the dehydration and after the rehydration. See Fig. 1 for further legends.

Sargassum thunbergii : The dehydration reduced the respiration rate (open circles in Fig. 3) appreciably but not seriously. The recovery of respiration rate occurring on the rehydration was remarkably well. Noticeably in addition, remarkable recovery and even promotion of respiration rate were observed on rehydration when the dehydration was intensive (closed circles in Fig. 3). Absorption of moisture under 100 % r.h. during 3 hours was scarce. Evolution of unidentified gas was also observed at 89.3 % dehydration. Experimental condition for this species are shown in Table 4.

Table 4. Experimental conditions for *Sargassum thunbergii*. See Table 2 for further legends.

Relative humidity	100	Control	100	75	50	75	50
Duration of desiccation	3	0	22	3	3	22	22
Degree of dehydration	−8.1	0	8.0	18.0	47.5	77.4	89.3

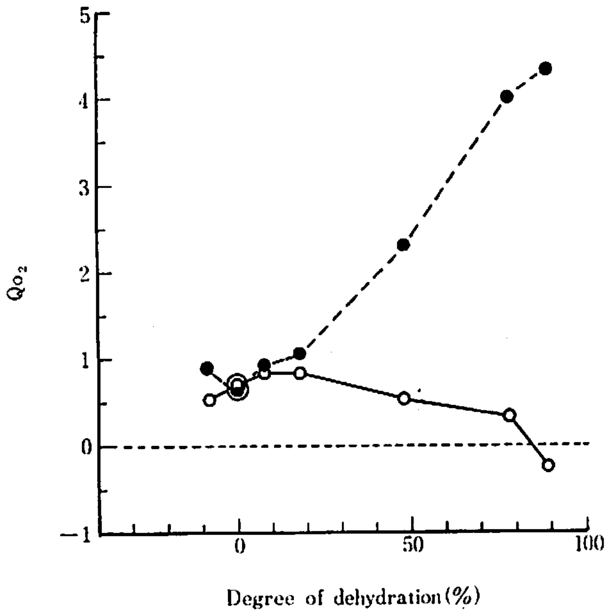


Fig. 3. Respiration rate in *Sargassum thunbergii* under the dehydration and after the rehydration. See Fig. 1 for further legends.

Ishige okamurai : General trend (Fig. 4) was similar to that in *Sargassum thunbergii* (Fig. 3). However, the reducing effect of dehydration and subsequent recovery by rehydration were less conspicuous than in *Sargassum*. Evolution of unidentified gas, though only little, was also observed at 89.3 % dehydration. Experimental conditions are shown in Table 5.

Table 5. Experimental conditions for *Ishige okamurai*. See Table 2 for further legends.

Relative humidity	100	Control	100	75	50	75	50
Duration of desiccation	2	0	20	2	2	20	20
Degree of dehydration	−15.1	0	9.4	9.6	39.8	76.0	89.3

Gelidium amansii : This deep sea alga (Fig. 5) appeared approximately similar to *Ulva* (Fig. 1) in the general trend. The dehydration (open circles in Fig. 5) reduced the respiration, and the recovery observed on rehydration (closed circles in Fig. 5) was very little. This common trend indicates that *Ulva* and *Gelidium* are considerably less tolerant to dehydration than the other species. Output of unidentified gas was

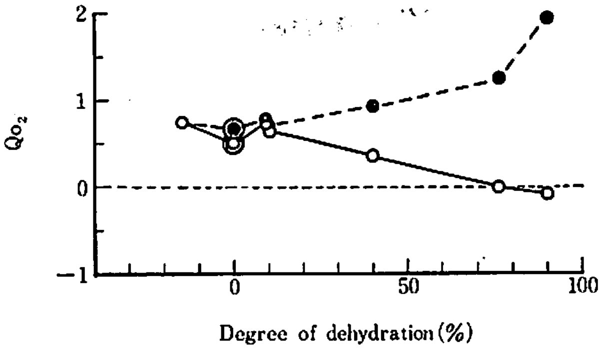


Fig. 4. Respiration rate in *Ishige okamurai* under the dehydration and after the rehydration. See Fig. 1 for further legends.

Table 6. Experimental conditions for *Gelidium amansii*. See Table 2 for futher legends.

Relative humidity	100	Control	100	75	75	50	50
Duration of desiccation	3	0	20	3	20	3	20
Degree of dehydration	−11.7	0	14.3	59	78	82.5	83.9

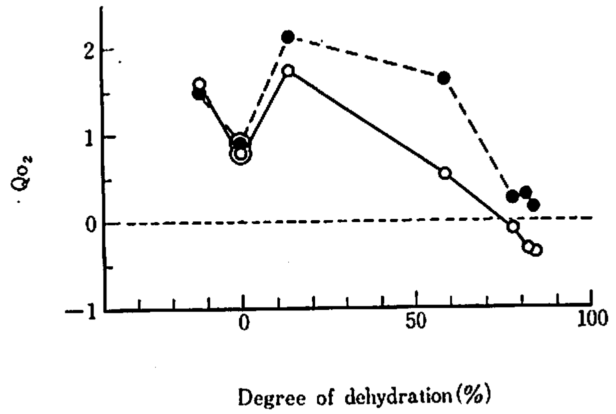


Fig. 5. Respiration rate in *Gelidium amansii* under the dehydration and after the rehydration. See Fig. 1 for further legends.

observed as well above 78 % dehydration. Experimental conditions are presented in Table 6.

Gracilaria verrucosa : Under the experimental conditions shown in Table 7, *Gracilaria* appeared the trend as seen in Fig. 6. General decline of respiration in dehydrated material was also observable and evolution of unidentified gas was slightly recognizable at 92.8 % dehydration (open circles in Fig. 6). Recovery was rather moderate (closed circles in Fig. 6).

Table 7. Experimental conditions for *Gracilaria verrucosa*. See Table 2 for further legends.

Relative humidity	100	100	Control	75	50	75	50
Duration of desiccation	2.5	20	0	2.5	2.5	20	20
Degree of dehydration	−3.9	−3.9	0	15.6	49.8	78.8	92.8

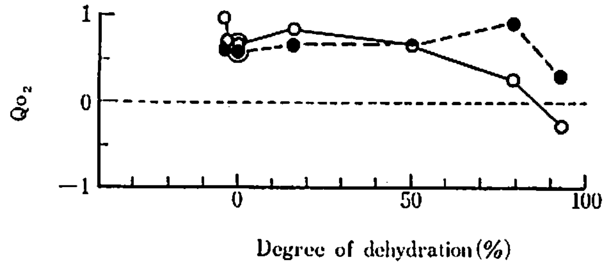


Fig. 6. Respiration rate in *Gracilaria verrucosa* under the dehydration and after the rehydration. See Fig. 1 for further legends.

Gloiopeltis tenax : General trend in this species (Fig. 7) was almost identical with that in *Gracilaria* (Fig. 6). Trend under excessive dehydration was also similar to that in *Gracilaria*.

Table 8. Experimental conditions for *Gloiopeltis tenax*. See Table 2 for further legends.

Relative humidity	100	Control	100	75	50	75	50
Duration of desiccation	3	0	20	3	3	20	20
Degree of dehydration	0	0	0	15.7	36.1	79.2	92.1

Laurencia okamurai : Fig. 8 shows the trend in *Laurencia okamurai* which has fragile construction of algal body. Weak dehydration as 11 % remarkably increased the O_2 uptake and the strong dehydration more than 33.3 % reduced it remarkably. Gas evolution observed in excessive dehydration was not found (open circles in Fig. 8). Recovery of respiration on the rehydration was not so remarkable, and did not occur at all when the dehydration was too strong such as above 83.3 % and for 22 hours (closed circles in Fig. 8).

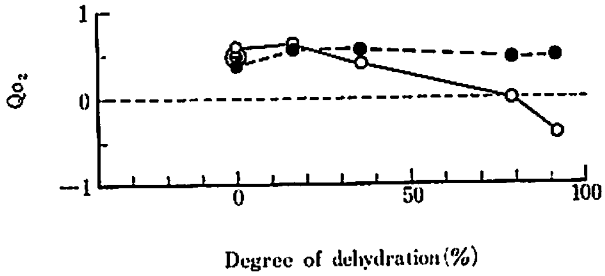


Fig. 7. Respiration rate in *Gloiopeltis tenax* under the dehydration and after the rehydration. See Fig. 1 for further legends.

Table 9. Experimental conditions for *Laurencia okamurai*. See Table 2 for further legends.

Relative humidity	100	Control	100	75	50	75	50
Duration of desiccation	3	0	22	3	3	22	22
Degree of dehydration	−11.2	0	11	33.3	48.3	83.3	91.6

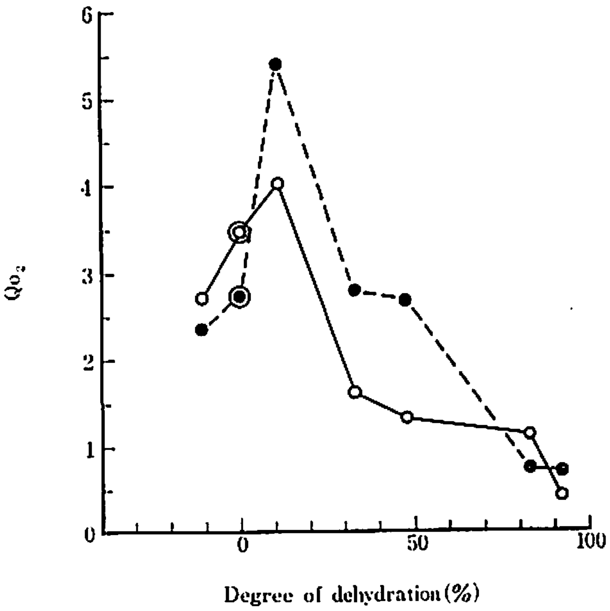


Fig. 8. Respiration rate in *Laurencia okamurai* under the dehydration and after the rehydration. See Fig. 1 for further legends.

This trend rather resembles that in *Gelidium amansii*, that is deep sea alga as *Gelidium* or fragile alga as *Laurencia* are apt to be seriously affected by strong dehydration. Experimental conditions are indicated in Table 9.

Zostera marina : This plant is a typical marine phanerogam in Japan. Respiration was gradually reduced by dehydration. The evolution of unidentified gas (open circles in Fig. 9) was shown when dehydrated as strongly as 88.5 %. Recovery of respiration on rehydration was not much conspicuous (closed circles in Fig. 9). Experimantal conditions are presented in Table 10.

Table 10. Experimental conditions for *Zostera marina*. See Table 2 for further legends.

Relative humidity	100	Control	100	75	50	75	50
Duration of desiccation	3	0	22	3	3	22	22
Degree of dehydration	−17.2	0	12.1	14.7	60.8	83.7	88.5

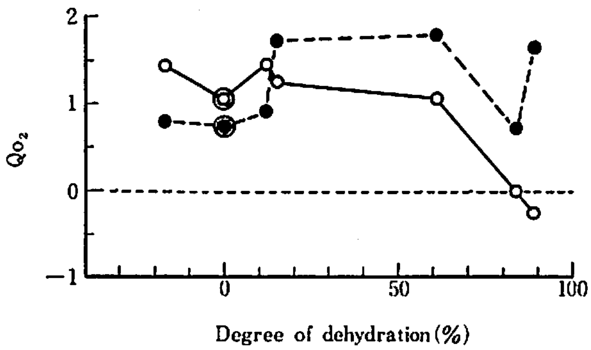


Fig. 9. Respiration rate in *Zostera marina* under the dehydration and after the rehydration. See Fig. 1 for further legends.

Zostera nana : General trend in *Zostera nana* (Fig. 10) under the experimental condition shown in Table 11 is quite identical with that in *Zostera marina* (Fig. 9).

Table 11. Experimental conditions for *Zostera nana*. See Table 2 for further legends.

Relative humidity	100	100	Control	75	50	75	50
Duration of desiccation	3	22	0	3	3	22	22
Degree of dehydration	−34.3	−8.3	0	0	12.9	81.3	91.3

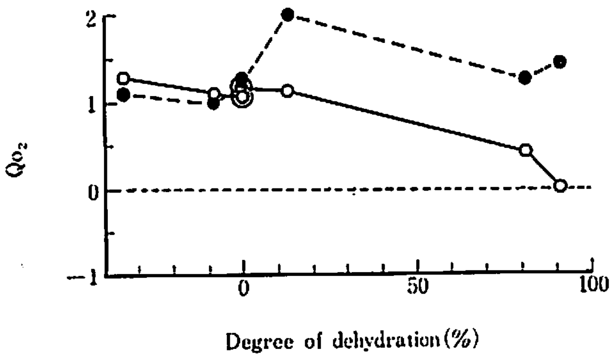


Fig. 10. Respiration rate in *Zostera nana* under the dehydration and after the rehydration. See Fig. 1 for further legends.

Table 12. Experimental conditions for *Potamogeton crispus*. See Table 2 for further legends.

Relative humidity	100	Control	75	100	50	75	50
Duration of desiccation	3	0	3	24	3	24	24
Degree of dehydration	−14.2	0	28.2	56.4	62.3	88.9	93.7

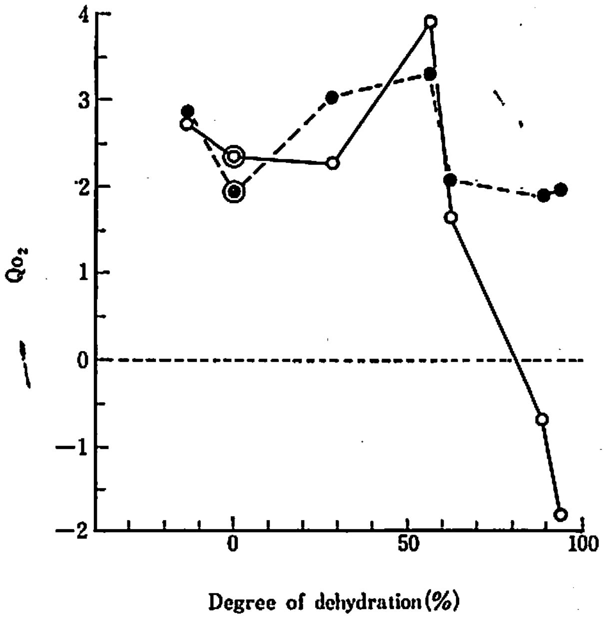


Fig. 11. Respiration rate in *Potamogeton crispus* under the dehydration and after the rehydration. See Fig. 1 for further legends.

Potamogeton crispus : General trend in this fresh water phanerogam is shown in Fig. 11. Slight dehydration such as 28.2 and 56.4 % caused the increase of Q_{O_2}, but strong dehydration as 88.9 % not only caused drastic decline but also caused evolution of unidentified gas (open circles in Fig. 11). Relative humidity as 93.7 % also caused remarkable evolution of gas as has been observed in all marine plant examined.

Table 13. Experimental conditions for *Ceratophyllum demersum*. See Table 2 for further legends.

Relative humidity	100	Control	75	50	100	75	50
Duration of desiccation	3	0	3	3	24	24	24
Degree of dehydration	−23.3	0	0	27.2	53.5	95.2	95.2

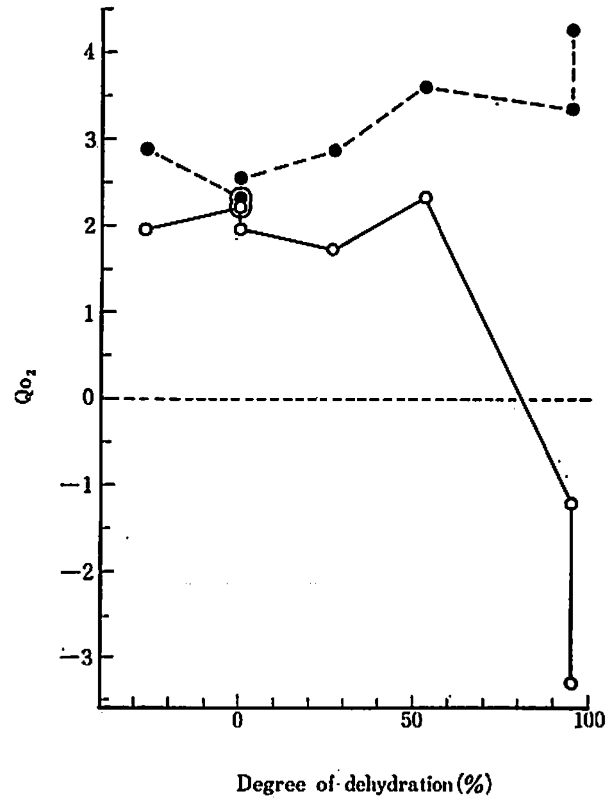


Fig. 12. Respiration rate in *Ceratophyllum demersum* under the dehydration and after the rehydration. See Fig. 1 for further legends.

The once depressed level of respiration remained almost unchanged even after the rehydration (closed circles in Fig. 11). Experimental conditions for this species are shown in Table 12.

Ceratophyllum demersum : The trend in O_2 uptake by the dehydrated materials rather resembels the case of *Potamogeton* as shown by open circles in Fig. 12. But the trend of recovery in this species was more conspicuous than that in *Potamogeton* as shown closed circles in Fig. 12.

Discussion

Perusal of the data obtained indicates a common trend in all the marine or fresh-water plants examined. That is, the plant undergoes recognizable O_2 uptake even under the condition without aqueous phase at all ; the O_2 uptake gradually declines as the dehydration proceeds as the results of water loss ; the O_2 uptake is sometimes enhanced by slight dehydration ; an unidentified gas is evolved when the dehydration extremely strong. Extent of the recovery of respiration after the rehydration varies from species to species. The difference appears to be closely related to the inherent characters, such as original habitat and structural fragility, of each plant, and also seems to reflect the tolerance to dehydration.

Bidwell and Craigie (1963) found the much reduced ability of *Fucus* to evolve CO_2 when not submerged. In this case the plant was exposed to air of saturated humidity. The experiment at low relative humidity and during long time was not measured by Bidwell and Graigie (1963). In the present work, measurements were made with the material placed in the air of 100 (saturated), 75, and 50 % relative humidity. In either work, however, the plants obviously showed declining respiration when drawn out of water. Ogata and Matusi (1963) reported that O_2 uptake by *Porphyra* steadily declined accompanying the proceeding loss of water by exposure to air. This fact is well consistent with the result of the present work.

The recovery of respiration occurring on the rehydration appeared to be different from species to species, and appearrd to reflect the difference in the tolerance to dehydration. That is, the algae living in lower part of intertidal zone or those having fragile construction are also sensitive to the dehydration, so since the recovery of O_2 uptake after rehydration is only little. Quite a similar paralellism was observed by Ogata and Takada (1968) in the case of tolerance to low salinity. *Gelidium*, rigid deep sea alga, and *Laurecia*, fragile alga, showed the weak tolerance to the low salinity.

Evolution of an unidentified gas is observed more or less in almost all the species when they are strongly dehydrated. Although being yet unidentified, this gas is presumably something other than CO_2 since it is not absorbed by the KOH in the central well of reaction flasks. Advance in the future will make the nature of this gas clear.

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Summary

Respiration in several marine and fresh-water plants was investigated with regard to the changes caused by dehydration and subsequent rehydration. O_2 uptake was observed even under exposure to air. The respiration gradually decline when the dehydration proceeded under exposure to low-humidity air and for prolonged time. Slight dehydration sometimes, but not always, caused a temporary enhancement of the respiration.

Evolution of an unidentified gas other than CO_2 was observed when the plants were dehydrated very strongly to such a degree as much as 90 % water loss of normal content. Recovery of once depressed respiration took place more or less after the rehydration of the dehydrated material. Extent of the recovery, often surpassing the initial rate, appeared to be a fairly good indication of the tolerance of each plant to dehydration. Some algae from deep sea bottom and those having delicate and fragile structure apparently showed less tolerance, in contrast to the others which are living in the intertidal zone or having sturdy structures.

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