

Comparative Study of the Effects of Temperature on Net Photosynthesis and Respiration in Lichens from the Antarctic and Subalpine Zones in Japan

YOSHIO INO

*Department of Biology, School of Education, Waseda
University, Shinjuku-ku, Tokyo 160*

Photosynthetic activity and dark respiration were measured in some species of lichens, *Umbilicaria*, *Cladonia*, *Stereocaulon*, *Usnea*, etc. sampled in the Antarctic and subalpine zones of central and northern Japan. On the basis of the responses of their activities to thallus temperature, the response patterns were divided into three groups, and further, each group was subdivided into some adaptation types for net photosynthesis and respiration. Lichens collected in the Antarctic were adapted to cool condition and some species collected in subalpine zones were adapted to warm condition. For example, the optimal temperatures for net photosynthetic rates in Antarctic lichens were lower than 5 C and those in lichens which lived on rock surface at a southern slope in mountains of Japan were higher than 20 C.

Key words: Antarctica—Lichen—Photosynthesis—Respiration—Subalpine zone—Temperature adaptation.

Photosynthetic activity is the primary factor in the growth of green plants, because the carbohydrate for their growth is produced by the photosynthesis. The growth patterns and the life modes of several plants have been made clear in consideration of the production rate and the distribution ratio of the produced matter. Generally, plants grow slowly in a severe environment, where one or some of the environmental factors, such as water, light, temperature, nutrients are insufficient for their growth.

The plant growth in such environments has been investigated by many ecologists; at desert, sand dune, alpine region, forest floor and other habitats. In the 1960's the arctic region was included in the areas for study of plant life in such environments and in the 1970's, the Antarctic which has the most severe environment for temperature on the earth, was included in the study areas.

The studies about the organisms in the Antarctic ecosystem have two faces. One is the study of life modes in severe environment and the other is the attempt to estimate the life modes of organisms at the glacial epoch. The number of the species and the biomass of the plants in the Antarctic ecosystem are limited by both low temperature and short growing period. Excepting vascular plants of two species

which lived at the Antarctic Peninsula, mosses and lichens on the naked land area along the coast, and algae in ponds, on moist gravel land and on snow and ice are the principal primary producers. Among the species of mosses and lichens which lived in the Antarctic, there are many species distributed over a wide area of the earth. It is suggested that their physiological activities, especially photosynthesis and respiration, are different with their habitats but there are few reports about comparative studies among geological strains (in *Polytrichum commune*, Sveinbjörnsson and Oechel, 1983).

The author stayed at East Antarctica in January and February 1982 as a member of 23rd Japanese Antarctic Research Expedition and measured the photosynthetic activities of moss communities which lived on East Ongul Island (69°00'S, 39°35'E) for the estimation of primary production of the Island (Ino, 1983a, b). He also collected some species of lichens which were one of the primary producers, and brought them to Japan.

The photosynthetic and respiration rates of these lichens were measured in the laboratory in October 1982. For the comparison, the activities of some species of lichens in Japan were measured. These rates were measured with an infrared gas analyzer under various conditions of temperature and radiation intensity. The response patterns of the activities to these factors differed with species.

Materials and Methods

Lichens used in this investigation were as follows.

Umbilicaria aprina and *Umbilicaria decussata*. They were black foliose lichens and collected on February 16, 1982 on the moraine neighboring Mt. Larsen (ca. 66°45'S, 50°40'E) in Enderby Land, Antarctica. *U. aprina* was collected in water-logged condition in a small stream on the shore of Richardson Lake and *U. decussata* attached to dry rock surface at the upper site of the moraine.

Usnea sulphurea. It was a black fruticose lichen and sampled in February, 1982 at two places in Antarctica. One place was in a small valley at Rundvågskollane (ca. 70°06'S, 38°40'E) in the face of Rützow-Holm Bay, where *U. sulphurea* 1 and 2 were sampled on February 1. *U. sulphurea* 1 was sampled on the shade side surface of rock, and it looked whitish green. *U. sulphurea* 2 was collected on the sunny side surface of rock. Another place was the leeward side of the dry rock in the moraine nearby Mt. Larsen and *U. sulphurea* was sampled here on February 16.

Usnea sulphurea and *Umbilicaria decussata* were in dry condition and they were stocked in freezer at -20 C after sampling. *Umbilicaria aprina* was in wet condition, therefore this sample was dried in the air for a few days and frozen at -20 C. Daily air temperatures in both regions ranged from 5 C to -10 C during the sampling period and it was guessed that the surface temperature of sunny rock was more than 20 C. Day length was ca. 21 hr and 18 hr at Rundvågskollane and Mt. Larsen, respectively.

Stereocaulon myriocarpum and *Cladonia tenuiformis*. They were collected in September, 1982 on the surface of rock in a small rocky area, embosomed with *Pinus pumila*, ca. 2 m in height and this place was on the south east slope near the top of Mt.

Tairoku (43°20'N, 142°38'E, and 1460 m alt.), central Hokkaido. This place was sunny but not windy and lichens were moist.

Stereocaulon sasakii, *Cladonia rangiferina*, *Cladonia stellaris*, *Parmelina crassata* and *Usnea diffracta*. These lichens were collected at a windy and rocky site on the northern slope of Mt. Kitayatsugatake (36°03'N, 138°21'E, and 2100 m alt.), central Japan, in October 1982. In this place, dwarf *Tsuga diversifolia*, *Rhododendron brachycarpum* and *Pinus pumila* were growing at crevices and concavities of rocks. *U. diffracta* hung from dead trees, *Tsuga diversifolia*, ca. 2 m in height, *P. crassata* attached on the bark of *Pinus pumila* and others were collected on the surface of rock.

After the samples were dried in the air, they were stored in the stock chamber until the measurement in October 1982. The inside of the chamber was held at 8°C and irradiated with fluorescent lamp affluent in red light. Light intensity was 100 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ or 6 klx.

Before the day of measurement, the lichens collected in the Antarctic were removed from the freezer to the stock chamber. The samples, both Japanese and Antarctic species, were remoistened with distilled water in the stock chamber before the day of measurement. At the beginning of the measurement, water was sprayed on the sample and waterdrops attached on thallus were eliminated by blotting paper.

The sample was placed in the black colored assimilation chamber, 6×5 cm area and 3 cm in depth, and covered with a transparent roof. The chamber was placed in the water whose temperature was controlled. Radiation was provided by incandescent lamp (500 W spot type) filtered through two layers of water filters, 6 cm and 12 cm respectively. Radiation intensity was varied from 800 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ to 0 at 6 steps with various kinds of white and black nets, and the intensities were measured with a Licor quantum probe. Temperature in the assimilation chamber was controlled with air which passed through a long pipe sunk in the water controlled its temperature. Thallus temperatures at upper and under surfaces and the air temperature in the chamber were measured with YSI precision thermister probes for surface temperature use.

An open gas analysis system was used and air which was taken from the roof, ca. 30 m high, was stored in a 0.6 m³ balloon for the depression of the fluctuation in CO₂ concentration. Air from the balloon was sent to the chamber at a flow rate of 0.80 l min⁻¹ but since no fans were incorporated within the chamber, parallel air circuits were connected across the chamber with a pump generating a flow of ca. 3 l min⁻¹ to reduce boundary layer resistances across the thallus surface. A small water room was prepared at the air gate of the chamber and maintained the thallus in a moist condition. The CO₂ concentrations in the air at the entrance and the exit of the chamber were measured alternately at 2 min interval with an infrared gas analyzer (Horiba 315 A).

The measurement began at the highest radiation intensity and the highest temperature. After the steady state in the difference of CO₂ concentrations was obtained, the experimental condition was changed to lower radiation intensity under the same temperature. It took an hour for a sequence of the measurement at different radiation

intensities, $800 \mu \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ to 0, and then, measurement began upon the second step of temperature.

Kappen (1983) reported that the photosynthetic activity of *Usnea sulphurea* sampled in the Antarctic was fully recovered after about 40 hr from the start of the experiment at Kiel, FR Germany. In our experiment, the recovery time could be reduced with the pretreatment. The photosynthetic activities under ca. $800 \mu \text{E} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ were saturated after a half-hour in Japanese lichens and those of Antarctic species required one or two hours.

The amount of material was 3 to 7 g fw. After the measurement of photosynthesis and dark respiration, a portion of sample was dried up for measuring dry weight and another part was homogenized with 90% acetone and the photosynthetic pigments were extracted. Chlorophyll a in the extract was determined spectrophotometrically (SCOR-Unesco W.G. 17, 1964).

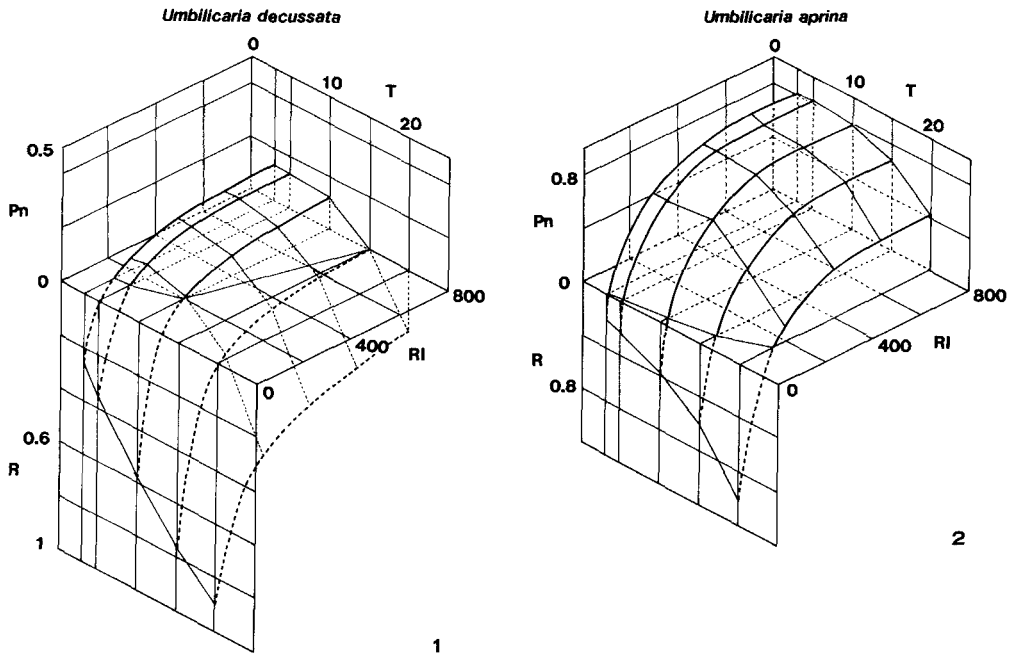
Results

Net photosynthetic rate was expressed as mg of CO_2 per mg of chlorophyll a per hour. It is sure that chlorophyll amount is a common indicator of the photosynthetic activity in different lichens, because it is difficult to measure the thallus area of fruticose lichen and the weight of crustose lichen. Chlorophyll a contents of samples are shown in Table 1. The contents were very low in comparison with those of higher plants (Kasanaga and Monsi, 1954), because a large portion of lichen is hyphae. There was a wide difference of contents among species, that is, the contents of *Usnea* with the

Table 1. Chlorophyll a and water contents of lichens used in the measurements of photosynthesis and dark respiration¹⁾

Species	Collected site	Chlorophyll a content $\text{mg} \cdot \text{g}^{-1} \text{dw}$	Water content at the end of experiment % of dw
<i>Usnea diffracta</i>	Mt. Kitayatsugatake	0.064	41
<i>Usnea sulphurea</i> 1	Rundvågskollane, Antarctica	0.124	115
<i>Usnea sulphurea</i> 2	Rundvågskollane, Antarctica	0.067	112
<i>Usnea sulphurea</i> 3	Mt. Larsen, Antarctica	0.077	82
<i>Parmelina crassata</i>	Mt. Kitayatsugatake	0.283	226
<i>Umbilicaria decussata</i>	Mt. Larsen, Antarctica	0.730	137
<i>Umbilicaria aprina</i>	Mt. Larsen, Antarctica	0.557	143
<i>Stereocaulon myriocarpum</i>	Mt. Tairoku	0.412	259
<i>Stereocaulon sasakii</i>	Mt. Kitayatsugatake	0.332	190
<i>Cladonia tenuiformis</i>	Mt. Tairoku	0.261	234
<i>Cladonia rangiferina</i>	Mt. Kitayatsugatake	0.142	85
<i>Cladonia stellaris</i>	Mt. Kitayatsugatake	0.091	108

¹⁾ These lichens were collected in the Antarctic and subalpine zones of Japan.

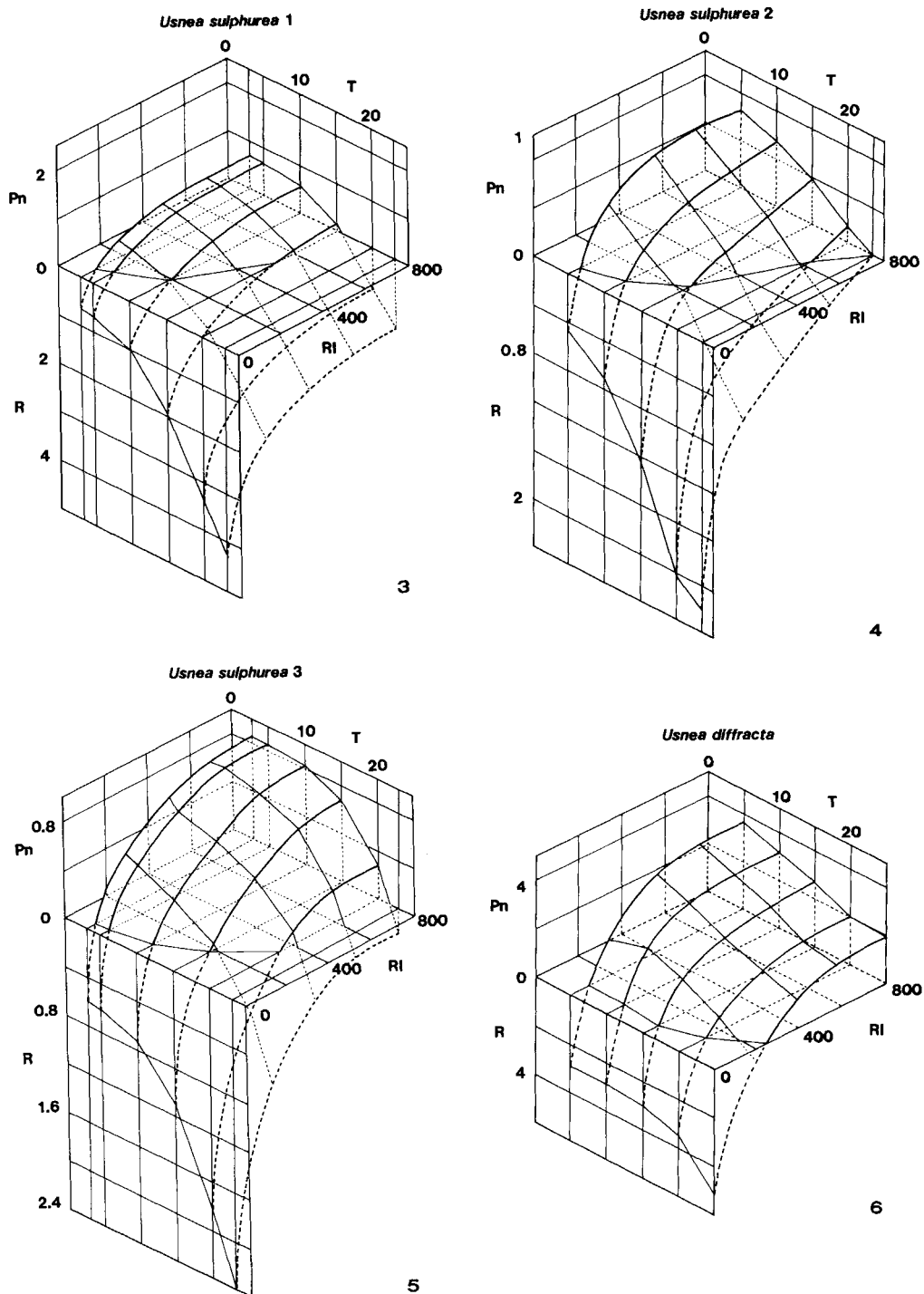


Figs. 1 and 2. Thallus temperature-related net photosynthesis at various radiation intensities and dark respiration in lichens. *Umbilicaria aprina* and *U. decussata* were collected in Antarctica. Pn: Net photosynthetic rate ($\text{mgCO}_2\cdot\text{mg}^{-1}\text{Chl a}\cdot\text{hr}^{-1}$). R: Dark respiration rate ($\text{mgCO}_2\cdot\text{mg}^{-1}\text{Chl a}\cdot\text{hr}^{-1}$). T: Thallus temperature (C). RI: Radiation intensity ($\mu\text{E}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$).

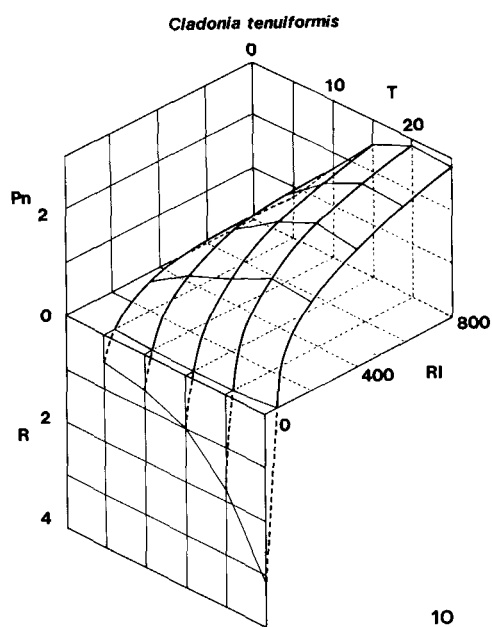
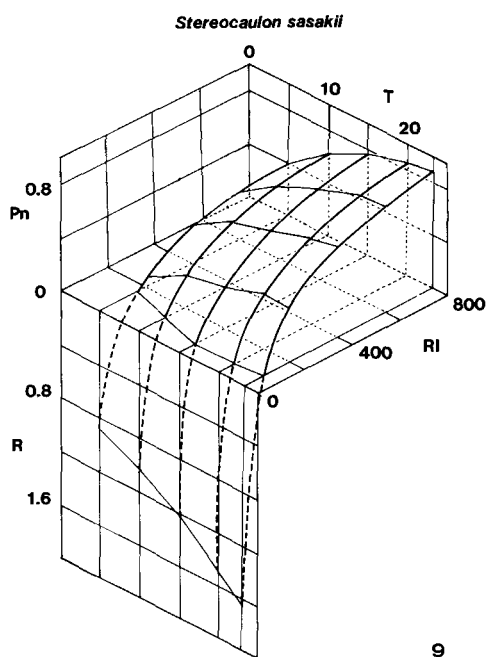
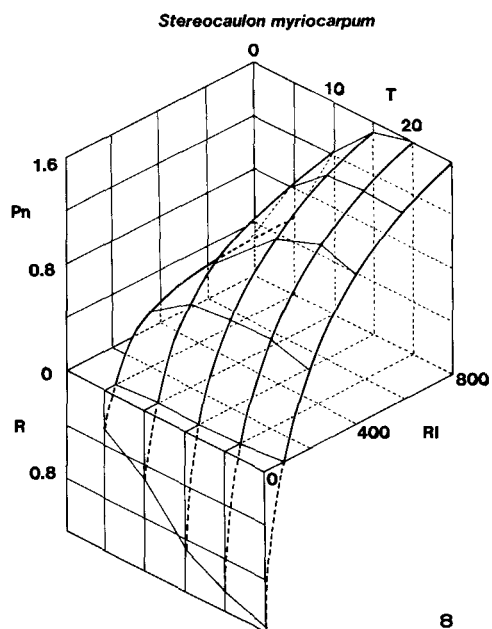
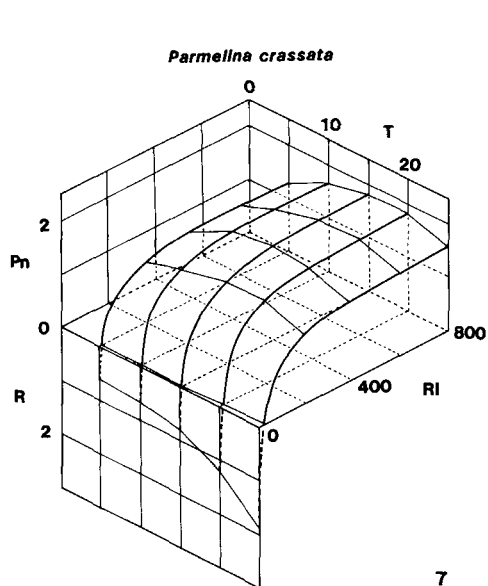
lowest content were about a tenth of those of *Umbilicaria*.

Photosynthetic and respiration rates at different temperatures and radiation intensities are shown in Figs. 1 to 12. The responses of photosynthetic and respiration rates of the lichens collected in the Antarctic shown in Figs. 1 to 5, clearly differed from those of Japanese lichens, that is, high net photosynthetic rates were observed in the low temperature range and the high temperature brought both low net photosynthetic rates and high respiration rates.

Net photosynthetic rate of *Umbilicaria decussata* was lower than those of others and was strongly suppressed at high temperature, that is, in the temperature range higher than 15 C, the net photosynthetic rate became negative. The net photosynthetic rates of *Usnea sulphurea* 1 and 2 were negative at 20 C and 23 C, respectively under all radiation intensities. The rate of *Umbilicaria aprina* did not become negative under the experimental condition but the rate continuously decreased at higher than 10 C. It is estimated that photosynthetic rates become a maximum at a temperature lower than 5 C and that the maximal rates reach almost $1.0\text{ mg CO}_2\cdot\text{mg}^{-1}\text{Chl a}\cdot\text{hr}^{-1}$. Respiration rates of *Usnea sulphurea* were considerably higher than those of *Umbilicaria* in all temperature ranges. Kappen (1983) measured, at Kiel, the photosynthesis and dark respiration rates of *Usnea sulphurea* which were collected at Victoria Land, Antarctica and reported that the net photosynthetic rate at $850\mu\text{E}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ and dark respiration rate was 1.35 and $2.5\text{ mg CO}_2\cdot\text{mg}^{-1}\text{Chl a}\cdot\text{hr}^{-1}$, respec-



Figs. 3-6. Thallus temperature-related net photosynthesis at various radiation intensities and dark respiration in lichens. *Usnea sulphurea* was collected in Antarctica and *U. diffracta* was collected in subalpine zone of Japan. Refer to Figs. 1 and 2 for abbreviations.



Figs. 7-10. Thallus temperature-related net photosynthesis at various radiation intensities and dark respiration in lichens. Materials were collected in subalpine zones of Japan. Refer to Figs. 1 and 2 for abbreviations.

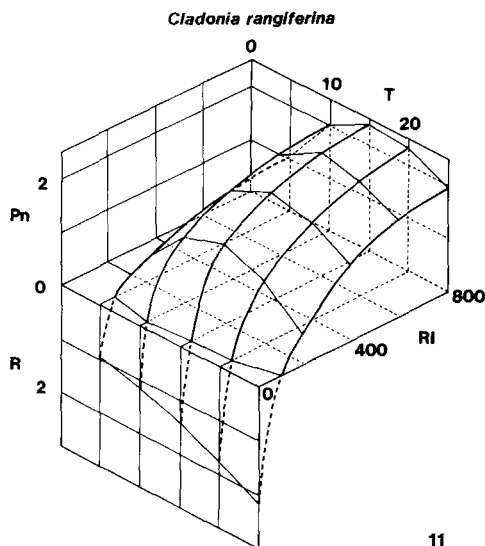
tively at 12 C. These rates were higher in photosynthesis and lower in respiration than those in this investigation.

Usnea diffracta (Fig. 6). It was estimated that the optimal temperature in the net photosynthetic rate was lower than 5 C and this characteristic differed from other Japanese lichens. Net photosynthetic rate did not become negative even at 25 C and this feature was different from those of Antarctic lichens. The net photosynthetic rate became the highest at 5 C, which was the highest among Japanese species, and the raise of temperature produced the decreasing of photosynthetic rate. Respiration rate was the highest among those of other species in all temperature ranges.

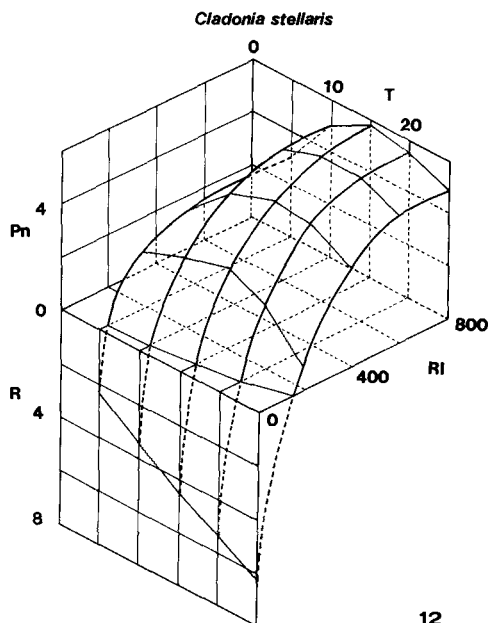
Parmelina crassata (Fig. 7). The change of net photosynthetic rate with the change of temperature was smaller than those of other species. Optimal temperature was 20 C and light compensation point was very low, that is, ca. $40 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ at 25 C and $10 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ at 5 C. Respiration rate increased rapidly at temperatures above 15 C.

Stereocaulon myriocarpum (Fig. 8). Net photosynthetic rate was a maximum at temperatures of 20 C and 25 C, under strong radiation intensity, but with the decrease of radiation intensity the optimal temperature dropped.

Stereocaulon sasakii (Fig. 9). The raise of temperature accelerated the photosynthetic rate and it was estimated that the optimal temperature for photosynthesis existed at a point higher than 25 C. At 5 C, net photosynthetic rate was down under dim light condition, $170 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$. Respiration rate rose rapidly above 15 C.



11



12

Figs. 11 and 12. Thallus temperature-related net photosynthesis at various radiation intensities and dark respiration in lichens. Materials were collected in subalpine zones of Japan. Refer to Figs. 1 and 2 for abbreviations.

Cladonia tenuiformis (Fig. 10). The net photosynthetic rate rose rapidly in strong radiation intensities with the increase of temperature, and the optimal temperature was ca. 20 C. Under low radiation intensity, the net photosynthetic rate was not rapidly accelerated with the raise of temperature, as shown at strong radiation intensity. Dark respiration rate was elevated rapidly at higher than 15 C.

Cladonia rangiferina (Fig. 11). The net photosynthetic rate rose from 5 C to 15 C with temperature and the rate decreased slowly above 15 C under all radiation intensities but dark respiration rate continuously increased with the raise of temperature.

Cladonia stellaris (Fig. 12). The net photosynthetic rate was higher than those of other species and it reached higher than $5 \text{ mg CO}_2 \cdot \text{mg}^{-1} \text{Chl a} \cdot \text{hr}^{-1}$ at 15 C and $600 \mu \text{E} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$. Dark respiration rates were also higher than those of others, especially at high temperature, and the rate was higher than $6 \text{ mg CO}_2 \cdot \text{mg}^{-1} \text{Chl a} \cdot \text{hr}^{-1}$ at 25 C.

Discussion

It seems that in the region where the environmental change is rapid and large, many organisms can adapt their physiological activities to the environmental change in a very short time. Lichens and mosses which attached to the surface of rocks, frequently are in dry condition and cease their physiological activities. After they absorb water in form of precipitation or fog, they return to life and their physiological activities, such as photosynthesis and respiration become active. If the recovery in physiological activities takes a lot of time, poikilohydric plants, as lichens and many mosses, cannot live in a place where environmental change is violent, because they dry up again in a short time. Lichens used in this investigation were collected in places whose environment had violent change, therefore it is sure that the recovery time of sample lichens is very short.

The relationships between the photosynthetic rate and the environmental factors such as temperature, radiation intensity and water content have been often studied. However, the relationships usually change with the method of sample treatment and measurement, therefore, when the photosynthetic activity of plants living in the field is measured in the laboratory, the efforts are made to demonstrate the maximal ability of the sample.

In the Antarctic, the optimal condition for physiological activities are suppressed considerably, therefore, the growth rates of plants are very slow (Hooker, 1980 ; Ino, 1983b ; Kappen, 1983). Lichens are often dried up in the field, therefore it is sure that the water content of thallus is an important factor in their activities. The relationship between photosynthetic activity and water content was studied under laboratory conditions by Kershaw and Rouse (1971), Kershaw (1972), Tegler and Kershaw (1980) and Kappen (1983).

Kershaw (1972) showed in his figures that the photosynthetic rates in several species at water saturation were 0% or near 0% of the maximum photosynthetic rates. There was no information about this phenomenon in his paper and it seems that his

results must be reexamined, because the diffusion rate of CO_2 through the hyphal layer to algae does not become 0, though it is lowered by the water amount around algae. Kappen (1983) showed that the photosynthetic rate in *Usnea sulphurea* was not suppressed at high water content.

It is very difficult to make certain this relation in ecophysiological viewpoint, because the water content of thallus generally changes in the course of the measurement of photosynthesis. This relation will be obtained in the experimental condition which the humidity of entrant air is controlled. In our experiment, the relationships between the photosynthetic and respiration rates, and the water content were not dealt with. The water contents of thalli at the end of the experiment were shown in Table 1 and they were probably near saturation.

Oechel (1976) investigated the temperature response of net photosynthesis and dark respiration in three species of arctic mosses at Barrow and he reported that there were the shifts in the maximum photosynthetic rate mainly caused by the change of moisture content and in the optimum temperature for photosynthesis during summer, June to August. Seasonal variations of photosynthetic activities were reported in several species of epiphytic mosses (Miyata and Hosokawa, 1961) and in *Cladonia* (Moser *et al.*, 1983). The former, who expressed photosynthetic efficiency in mg of CO_2 per g of dry weight per hour described that the general trend in the change of the maximum photosynthetic rate was approximately consistent with that of the chlorophyll content, and the latter concluded that photosynthetic activity in *Cladonia* closely paralleled atmospheric moisture status. In our experiment, chlorophyll content and water content were eliminated from the limiting factors for photosynthesis,

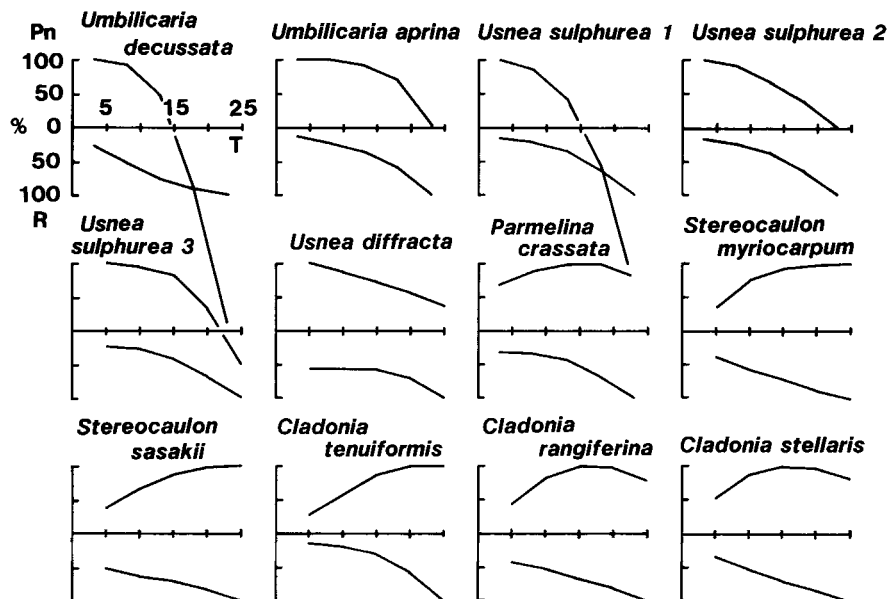


Fig. 13. Thallus temperature-related net photosynthesis at saturated radiation intensity and dark respiration in lichens. The rates were expressed in relative values to the maximum rates.

because the photosynthetic rate was expressed per chlorophyll *a* amount and usually measured under the condition of near water saturation. Therefore, the response patterns obtained in this investigation were worthy to be discussed.

In Fig. 13, the responses of the saturated net photosynthetic rates and the dark respiration rates to different temperatures were drawn in relative values to the maximal net photosynthetic rates or respiration rates. There were differences in the temperature response patterns among species and these patterns were divided into three patterns, that is, the pattern having higher net photosynthetic rate in the high temperature range (Pn rise pattern), the pattern having lower net photosynthetic rate in the high temperature range (Pn down pattern) and the pattern having maximum net photosynthetic rate from 5 C to 25 C (Pn convexity pattern).

Generally, it is said that the velocity of chemical reaction is accelerated about two times with the rise of each 10 C ($Q_{10}=2$). It is considered that photosynthesis and respiration are chemical reactions; therefore, if other factors, especially radiation intensity, which effect these rates are satisfied for these reactions, photosynthetic rate and respiration rate may be accelerated with the rise of temperature according to the velocity coefficient 2.

As shown in Fig. 13, there are three patterns in the responses of net photosynthetic rate with the rise of temperature. These patterns are caused by the relation between gross photosynthetic rate and dark respiration rate with temperature. The velocity coefficient for net photosynthesis and dark respiration in each species were calculated with the gradients of the changes of net photosynthetic and dark respiration rates.

Pn rise pattern and Pn down pattern are divided severally into four types. When the mean velocity coefficient of net photosynthetic rate in a lichen from 5 C to 25 C or 23 C is more than 2, this lichen was regarded to be adapted to warm temperature in net photosynthesis. In the types for which net photosynthetic rate became high with the rise of temperature, if velocity coefficient of gross photosynthesis largely exceeded that of dark respiration, it was considered that the net photosynthetic activity adapted to warm condition. The rapid increase of dark respiration with the rise of temperature become a suppression factor to growth; therefore when the mean velocity coefficient of respiration was smaller than 2, it was considered that the respiration activity adapted to warm condition. When the mean velocity coefficient in net photosynthesis was larger than 2, and that in dark respiration was smaller than 2, this species was regarded as a warm adaptation type in both net photosynthesis and dark respiration. If gross photosynthesis is not accelerated with the rise of temperature, the net photosynthetic rate in low temperature range becomes higher than that in high temperature range, because respiration rate becomes low with falling of temperature. It can be said that this characteristic is very suitable for the growth in cool temperature condition.

In the case that temperature-net photosynthetic curve has a maximal point, that is, Pn convexity pattern, the existence of adaptation cannot be discussed with the above mentioned criterion. In this pattern, the characteristics that the respiration rate decreases rapidly with the drop of temperature and that it increases slowly with the rise of temperature, are suitable for the growth.

Table 2. Adaptation types of net photosynthetic and respiration activities to the rise of temperature from 5 C to 25 C¹⁾

Change patterns in Pn	Adaptation types	Mean velocity coefficient from 5 C to 25 C		Species
		Pn	R	
Pn rise	wPn	> 2	>2	<i>Stereocaulon sasakii</i> <i>Stereocaulon myriocarpum</i>
	wR	< 2	<2	
	w(Pn•R)	> 2	<2	<i>Cladonia tenuiformis</i> <i>Cladonia stellaris</i> <i>Cladonia rangiferina</i> <i>Parmelina crassata</i>
	non	< 2	>2	
Pn convexity				
Pn down	cPn	< -2	<2	<i>Usnea sulphurea</i> 1, 2 & 3 <i>Umbilicaria decussata</i> <i>Umbilicaria aprina</i> <i>Usnea diffracta</i>
	cR	> -2	>2	
	c(Pn•R)	< -2	>2	
	non	> -2	<2	

¹⁾ These types were decided on to compare the changing rates in net photosynthesis and respiration with $Q_{10}=2$ in chemical reaction velocity. For example, wPn type means that lichen is adapted to warm condition, c(Pn•R) type means that lichen is adapted to cool condition in net photosynthetic rate and respiration rate, and 'non' type means that lichen is not adapted.

It is not clear that the all adaptation types exist in the field but lichens used in this experiment could be classified into some subtypes (Table 2). Two species of *Stereocaulon* were warm adaptation type, although they were collected at subalpine zone. It may be caused by the fact that the surface temperature of the rock in southern slope rises in the daytime. *Cladonia tenuiformis* was Pn rise pattern, but this species was considered as a non-adaptation type. *Cladonia stellaris*, *C. rangiferina* and *Parmelina crassata* belonged to Pn convexity pattern. Three species collected in the Antarctic were adapted with regard to both net photosynthesis and respiration to cool temperature. *Usnea diffracta* collected on the top of a dead tree in subalpine zone was Pn down pattern but it was not recognized as cool adaptation type. It is possible to estimate the adaptability for photosynthesis and respiration to the temperature in the habitat with such methods.

This conjecture will be available about such simple morphological plants, as lichens and some mosses. About higher plant whose photosynthetic activity is effected by many physiological factors, such as stomatal opening, water transport and water absorption, simple response pattern will not apply.

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