ORIGINAL ARTICLE

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Predicting the impact of climatic warming on the carbon balance of the moss *Sanionia uncinata* on a maritime Antarctic island

Abstract The effects of climatic factors, especially those of temperature, on the carbon balance of the moss *Sanionia uncinata* were examined on King George Island in the maritime Antarctic. Net photosynthesis (P_n) and dark respiration rates of two colonies (A and B) were measured with a portable infrared gas analyzer. Colony A showed small P_n compared with its dark respiration rates throughout the growing season. Colony B showed much higher net photosynthetic rates, but the dark respiration rates of the two colonies did not differ significantly. Net photosynthetic rate determined at light saturation was almost constant over a wide temperature range, from 5° to 15°C, while the dark respiration was strongly affected by temperature. To assess the impact of warming on the carbon balance of the moss, cumulative carbon gain of the moss was calculated using a simulation model for the main part of the growing season. The results suggest that climatic warming may cause a reduction of carbon gain in some relatively photosynthetically inactive moss colonies.

Key words Antarctic · Carbon balance · Climatic warming · Moss · Photosynthesis · *Sanionia uncinata*

Introduction

It is generally considered that high-latitude ecosystems are particularly sensitive to climatic change due to the short growing season and the predominance of permafrost. Current global warming predictions indicate that the maximum annual mean warming will occur in high northern latitudes (IPCC 2001). Recently, a number of studies have been conducted to predict the impact of climatic change on boreal and arctic ecosystems, because these ecosystems have a large carbon stock that would affect the global carbon cycle (Kojima 1994; Oechel and Vourlitis 1994; Oechel et al. 2000).

By contrast, relatively little attention has been paid to the impact of climatic change on Antarctic terrestrial ecosystems, probably due to the small carbon stocks and to the less-pronounced warming predicted by modeling studies (IPCC 2001). However, there is some evidence that air temperatures in Antarctic regions have increased markedly over the last century (Jones 1990). Some global climate models predict that a warming larger than 3°C is likely to occur in the Antarctic by the end of the twenty-first century (Wu et al. 1999).

Although information about the impact of climatic change on Antarctic terrestrial ecosystems is sparse, reported studies so far have indicated that climatic changes have a significant effect on these ecosystems. Smith (1994) reported that the numbers of individuals of two native Antarctic vascular plants, *Colobanthus quitensis* (Kunth) Bartl. and *Deschampsia antarctica* Desv., have increased over the last 27 years in the maritime Antarctic. He suggested that this increase was a response to a warming trend in summer air temperatures that has been evident since the late 1940s. Kennedy (1996), who integrated the results of fumarole (volcanic vent) observations, field manipulation studies, and laboratory incubation experiments, suggested that increased abundance, growth, and structural heterogeneity of Antarctic fellfield communities were generic responses to elevated temperature and moisture.

However, climatic warming may also have negative effects on some Antarctic plants. It has been reported that Arctic plants adapted to low-temperature habitats are likely to be disadvantaged in other temperature regimes due to increased respiration maintenance costs (e.g., Crawford 1989). This may also apply to Antarctic plants. Ino (1985) reported that the net photosynthetic rate of the Antarctic lichen *Umbilicaria decussata* (Vill.) Zahlbr. was strongly suppressed by high temperatures, showing negative values at temperatures higher than 15°C. Low optimum temperatures (less than 10°C) of net photosynthesis (P_n) have been

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reported for many Antarctic lichens (Kappen 1983; Kappen and Friedmann 1983; Ino 1985) as well as some Antarctic bryophytes (Kappen et al. 1989). These facts suggest that a cool climate is important for these plants to maintain a positive carbon balance and that climatic warming may reduce their carbon gain.

This study aimed to clarify the effects of climatic factors, especially those of temperature, on the carbon balance of the moss *Sanionia uncinata* (Hedw.) Loeske [= *Drepanocladus uncinatus* (Hedw.) Warnst.], which is the most abundant moss species on King George Island in the maritime Antarctic. For this purpose, I examined the effects of environmental factors on the P_n and dark respiration (R) of the moss. The impact of climatic warming on the carbon balance of the moss was subsequently estimated using a simulation model.

Materials and methods

Study site and materials

Great Wall Station (Chinese Antarctic Station) is situated on the Fildes Peninsula of King George Island in the South Shetland Islands (62°12'S, 58° 57'W). Monthly mean air temperatures, measured in the meteorological observation site at the Great Wall Station, in November 1990, December 1990, and January 1991, were −1.3, 0.1, and 2.0°C, respectively. There were 25, 22, and 24 days of precipitation each month, respectively (Chinese National Antarctic Research Expedition, unpublished data). Most of the precipitation occurred as rain from the end of December to January.

On King George Island, *Sanionia uncinata* is found in a wide variety of habitats, ranging from exposed rock surfaces to wet sites near streams (Lindsay 1971; Nakatsubo and Ohtani 1992). The length of the snow-free season among the habitat types also varies widely. In this study, a rock (15 m × 10 m) situated by the seashore near the Great Wall Station was selected as the study site because it provided *S. uncinata* with a range of habitat types. Snow melt tended to occur earlier on the upper portion of the rock than on the side face. Two colonies of *S. uncinata* growing on different portions of the rock were used for the measurements. Colony A covered the upper horizontal surface of the rock; Colony B grew on the southwest-facing side of the rock. Because sporophytes of *S. uncinata* have not been found in this area, these colonies were assumed to be clones. Colony B was covered with snow until the middle of December, while Colony A was free of snow from at least the end of November. A third colony (Colony C) growing on a flat, gravelly site near the Great Wall Station was also used to study the relationship between moisture conditions and photosynthetic activity.

During the snow-free season, temperature in the upper green layer (about 5 mm depth) of Colony A was measured using a datalogger with a thermistor sensor (Kadec-U; KONA System, Sapporo, Japan). At the same time, photosynthetic photon flux density (PPFD) was recorded in the meteorological observation site at the Great Wall Station using a datalogger (Kadec-UP; KONA System) with a quantum sensor (LI-190SA; LI-Cor, Lincoln, NE, USA).

Gas exchange measurements

A preliminary study showed that the photosynthetic capacity of the moss differed widely between colonies (see below). However, it was impracticable to measure a large number of samples because of the small size of each colony and the rainy weather prevailing in this region. Therefore, instead of taking a large number of samples, a quadrat of 50 cm × 50 cm was positioned in the central part of each colony, and all samples used in the measurement were taken from the quadrat to minimize within-colony variation in physiological activities.

The samples were collected on 7, 15, and 27 December 1990, 11 and 23 January 1991, and 7 February 1991. Core samples of pure stands of *S. uncinata*, 9 cm in diameter, were taken from the colonies. The brown lower portion of the sample was discarded and the green layer of each core sample (about 1 cm thick) was placed on a plastic petri dish. The fresh samples were weighed to determine the tissue water content in the field. If the samples were dry, they were wetted with water 1 day before the measurements. The samples were stored outside until the gas exchange measurements were made. Unless otherwise stated, measurements of P_n were carried out within 24 h of collecting the sample.

P_n and R were measured using an open-circuit gas exchange system with a portable infrared gas analyzer (KIP-8510; Koito, Yokohama, Japan) and a temperature-regulated assimilation chamber with a volume of 0.6 l. All gas exchange measurements were carried out in the field under natural solar radiation. Unless otherwise stated, moss samples were wetted with water to near water saturation just before the measurement. At any one time, one petri dish with moss sample was placed in the chamber.

To study the effect of photon flux density on P_n, PPFD was decreased in a stepwise fashion from full solar radiation to dark by covering the chamber with polyethylene sheets, paper sheets, or aluminum foil. Temperature of the samples was maintained at 10°C.

The effects of temperature on P_n and R were studied by controlling the temperature in the chamber. During this measurement, PPFD in the chamber was maintained at 600 ± 50 μmol m^{-2} s^{-1} by covering the chamber with polyethylene sheets of various thicknesses.

To study the effects of moisture conditions on the net photosynthetic activity, the light–photosynthesis curves of one sample collected from Colony C were determined at three water contents: 280% dw, 690% dw, and 1060% dw.

The recovery of photosynthetic activity from desiccation was examined as follows. A sample was collected from a naturally dried colony (Colony C) on 25 January. The net photosynthetic rate of this sample was determined at the field water content in the manner described above. The

sample was then fully wetted with water and the time course of recovery monitored.

After the gas exchange measurement, the samples were air dried and brought to Japan. To obtain the dry weights, they were then oven dried at 80°C to a constant weight. The water content of the sample was calculated as follows:

Water content (%) = (fresh weight − dry weight)/
dry weight × 100

Results

Microclimatic conditions

Figure 1 shows PPFD and moss temperature in the upper green layer of Colony A during the main growing season (from 21 December 1990 to 31 January 1991). Daily maximum mo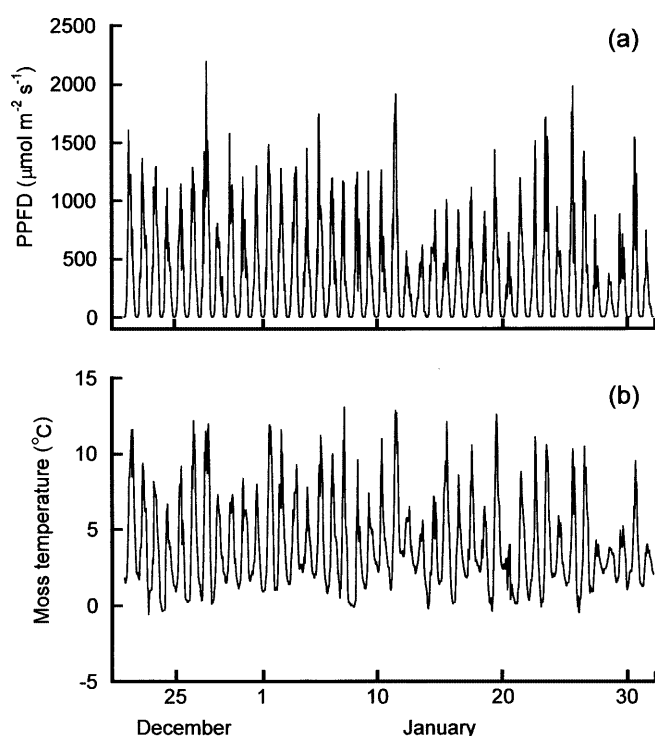ss temperatures never exceeded 15°C during this period but they showed considerable day-to-day variation. On the other hand, minimum temperatures were within a narrow range, from −1°C to 3°C. These results agree well with the data of Davey et al. (1992), who examined temperatures within soil and plant habitats on Signy Island in the maritime Antarctic (60°43'S). At the study site on King George Island, most of the *Sanionia* colonies, including Colonies A and B, were totally covered with snow by the end of February, in 1991.

The maximum PPFD during the summer season exceeded $1500 \mu mol \, m^{-2} s^{-1}$ on fine days (Fig. 1a). From 12 January 1991, however, the daily maximum PPFD was usually below $1000 \mu mol \, m^{-2} s^{-1}$ because of the rainy (snowy) weather.

During the summer season (from early December to early February), the water content of Colony A was usually within the range of 360% to 850%, although this dropped to 190% in late December (Table 1). The sample collected from Colony B under the snow cover showed a relatively high water content (770%), but once the snow cover disappeared, the water content of Colony B fluctuated within a low moisture range, from 90% to 280% (Table 1).

Photosynthesis and respiration

Table 2 shows the P_n and R of Colonies A and B during the summer season. Net photosynthetic rates were determined at PPFDs of $400 \pm 50 \mu mol \, m^{-2} s^{-1}$, because the PPFD in the assimilation chamber did not exceed this level on cloudy days. Colony A showed a relatively small net photosynthetic rate compared with the R rates. At 10°C and $400 \pm 50 \mu mol \, m^{-2} s^{-1}$ PPFD, the absolute values of net photosynthetic rates of Colony A were always smaller than those of the R, with an average P_n/R ratio smaller than 0.6 (Table 2). As a result, the light compensation point was relatively high, about $80 \mu mol \, m^{-2} s^{-1}$ (Fig. 2). This light compensation point is much higher than those reported for other moss species (Lösch et al. 1983; Alpert and Oechel 1985; Kappen et al. 1989). Net photosynthetic rates determined in December and those determined late in the growing season (January and early February) did not differ significantly (*t*-test; $P > 0.05$, $n = 3$).

The net photosynthetic rate of Colony B in early summer could not be determined because of the prolonged snow cover. After the snow melt, on 27 December, 11 and 23 January, and 7 February, Colony B showed a higher net photosynthetic rate and P_n/R ratio than did Colony A

Fig. 1. Photosynthetic photon flux density (*PPFD*) (**a**) and moss temperature (**b**) in the upper green layer (about 5 mm depth) of Colony A during the main growing season (from 21 December 1990 to 31 January 1991)

Table 1. Field water content of the two *Sanionia uncinata* colonies in the 1990–1991 summer season

Colony	Water content (%)[a]					
	7 December	15 December	27 December	11 January	23 January	7 February
A	540	360	190	760	850	510
B	–	770[b]	210	170	280	90

[a] Water content = (fresh weight − dry weight)/dry weight × 100%
[b] The colony was covered with snow

Table 2. Net photosynthetic rate (P_n) and dark respiration rate (R) at 10°C of the two *Sanionia uncinata* colonies[a]

Colony	P_n (mg CO_2 g^{-1} h^{-1})[b]		R (mg CO_2 g^{-1} h^{-1})		P_n/R	
	December	January–February	December	January–February	December	January–February
A	0.448 (0.070)	0.451 (0.109)	0.824 (0.051)	0.814 (0.084)	0.56 (0.11)	0.58 (0.17)
B	–	0.777 (0.038)	–	0.879 (0.017)	–	0.88 (0.03)

[a] Each value is the mean of three determinations with SE in parenthesis
[b] Determined at $400 \pm 50\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ PPFD
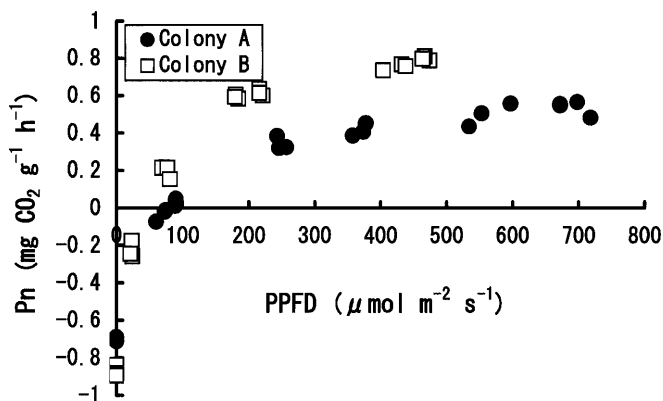
Fig. 2. Net photosynthesis (P_n) of two *Sanionia uncinata* colonies (A and B) at different PPFD at 10°C (11–12 January 1991)
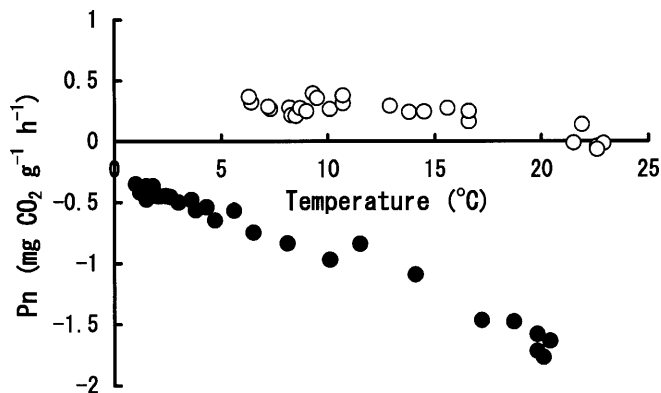

Fig. 4. Net photosynthesis (P_n) of *Sanionia uncinata* (Colony C) at different tissue water contents and PPFDs (15–16 January 1991)

Fig. 3. P_n (*open circles*) and dark respiration (R; *closed circles*) of *Sanionia uncinata* at different temperatures. The P_n was measured at $600 \pm 50\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ PPFD (18 December 1990)

(Table 2; Fig. 2). The difference in P_n between the two colonies was significant (paired *t*-test; $P < 0.05$, $n = 4$). In contrast, R rates of the two colonies did not differ significantly (paired *t*-test; $P > 0.05$, $n = 4$).

At light saturation, the net photosynthetic rate of Colony A determined on 18 December was nearly constant within a wide temperature range from 5° to 15°C (Fig. 3). This was also true for the sample collected from Colony A on 8 December and that collected from Colony B on 13 January (data not shown). Conversely, R rate was strongly affected by temperature. The Q_{10} value for dark respiration was calculated to be 2.1.
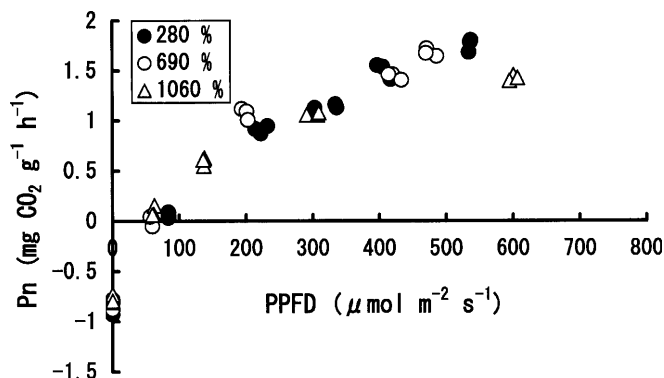
Figure 4 shows the light-photosynthesis curves of *S. uncinata* (Colony C) determined at three water contents: 280%, 690%, and 1060%. Although a slight decline in net photosynthetic rate was observed at the highest water content, the rates at 280% and 690% did not differ significantly, indicating that the optimum range of water content for P_n is broad. This agrees with the result of Collins (1977), who examined the effect of water content on the net photosynthetic rate of *S. uncinata* on Signy Island.

On 25 January, the tissue water content of Colony C dropped below 160% in the field. The net photosynthetic rate of the sample at the field water content was near the detection limit of the infrared gas analyzer system (0–20 min in Fig. 5). Net photosynthetic activity soon recovered after rehydration; positive P_n was recorded from 20 min after the rehydration (Fig. 5). A rapid increase in the net photosynthetic rate was observed for about 40 min, but after that period the rate increased only gradually. The rate measured on the following day was almost twice as high as that recorded 40 min after rehydration (data not shown).

The effect of temperature on the carbon balance

The data of the present study showed that the photosynthetic activity of some moss colonies in the study area was low compared to their respiratory activity and that the increase of respiration with temperature was steeper than the increase of P_n with temperature. These observations suggest that conditions of low temperature are important for the
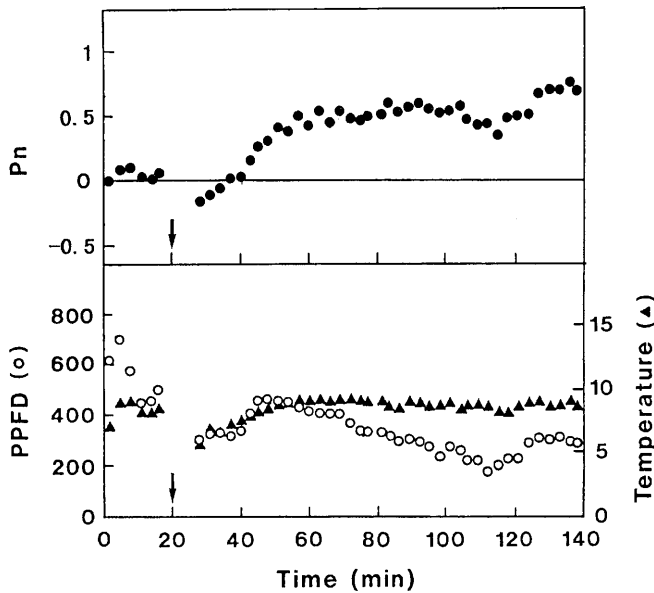
Fig. 5. Recovery of net photosynthesis (P_n; mg CO_2 $g^{-1}h^{-1}$) after rehydration. Dry moss sample (water content = 160%) was collected from Colony C and wetted with water to 1100% on 25 January 1991. *Arrows* show the time when the sample was wetted

Table 3. Parameters used in the calculation of the cumulative carbon gain of the two *Sanionia uncinata* colonies[a]

Colony	$P_n(10)$[b]	$R(10)$[c]	S[d]
A	0.482	0.828	0.0079
B	1.011	0.873	–

[a] Each value is the mean of the values determined on 28–29 December, 11–12 and 23–25 January in the 1990–1991 summer season
[b] Net photosynthetic rate at light saturation and 10°C (mg CO_2 $g^{-1}h^{-1}$)
[c] Dark respiration rate at 10°C (mg CO_2 $g^{-1}h^{-1}$)
[d] Coefficient of the light–photosynthesis curve

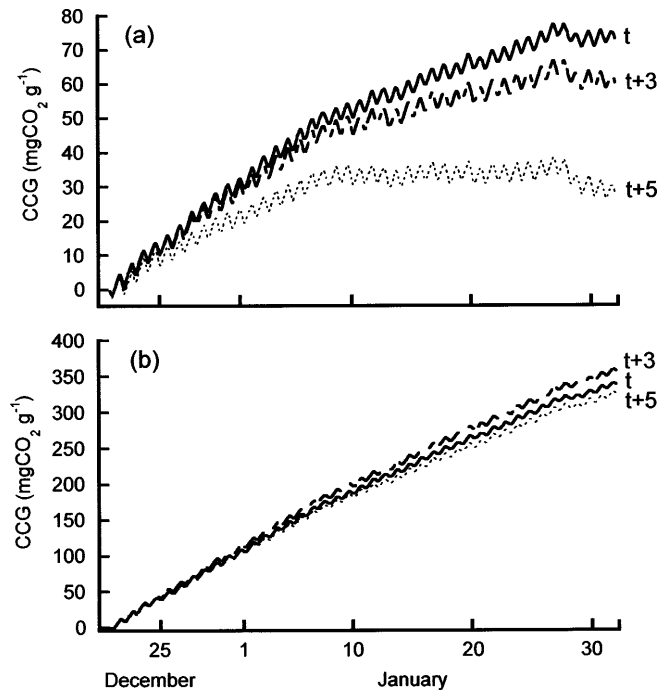**Fig. 6.** Cumulative carbon gain (*CCG*) of *Sanionia uncinata* at present temperatures (*t*) and under two warming conditions (*t* + 3°C and *t* + 5°C). **a** Colony A, and **b** when net photosynthetic rate P_n (10) and $R(10)$ of Colony B were used in the same calculation

moss to maintain a positive carbon balance and that climatic warming would reduce the carbon gain of the moss by increasing respiratory loss. To assess the impact of warming on the carbon balance of the moss, cumulative carbon gain (*CCG*) of Colony A was calculated for the main part of the growing season, from 21 December 1990 to 31 January 1991, when temperature data of the colony were available.

The *CCG* was calculated using the following nonlinear, multiple regression model (Kume and Ino 1993):

$$CCG = \int P_n(i,t)\mathrm{d}h = \int \left(P_g(i,t) - R(t)\right)\mathrm{d}h$$

$$P_g(t) = P_n(t) + R(t)$$

$$P_n(t) = P_n(10) \times \left(at^2 + bt + c\right)$$

$$R(t) = R(10) \times Q_{10}^{(t-10)/10}$$

$$P_g(i) = P_g(10)\left(1 - e^{-Si}\right)$$

$$P_g(i,t) = P_g(t)P_g(i)/P_g(10)$$

where $P_n(i,t)$ is the net photosynthetic rate at i $\mu mol\,m^{-2}s^{-1}$ PPFD and t°C (mg CO_2 $g^{-1}h^{-1}$); $P_g(i,t)$ is the gross photosynthetic rate at i $\mu mol\,m^{-2}s^{-1}$ PPFD and t°C (mg CO_2 $g^{-1}h^{-1}$); $P_n(t)$ is the net photosynthetic rate at light saturation and t°C; $R(t)$ is the respiration rate at t°C; $P_n(10)$ is the net photosynthetic rate at light saturation and 10°C; $R(10)$ is the respiration rate at 10°C. S is the coefficient of the light-photosynthetic curve; h is the time (hours) over which the net photosynthetic rate and *CCG* are calculated; and a, b, c are coefficients of the temperature–photosynthetic curve and were calculated from Fig. 3 to be −0.0061, +0.1169, and +0.4474, respectively ($r^2 = 0.81$). The Q_{10} calculated from the temperature–respiration curve (Fig. 3) was 2.1. The parameters $P_n(10)$, $R(10)$, and S were deter-

mined on 28–29 December, 11–12 January and 23–25 January, and the mean value of each parameter was used in the calculation (Table 3). Although these parameters were determined at water saturation, no correction for water content was made. In this model, both $P_g(i,t)$ and $R(t)$ are likely to be underestimated due to the occurrence of photorespiration. However, because $P_n(i,t)$ was obtained by subtracting $R(t)$ from $P_g(i,t)$, the effect of photorespiration on *CCG* is assumed to be small.

Hourly data of moss temperature (at about 5 mm depth) and PPFD recorded at the meteorological field were used as t and i, respectively. To assess the impact of climatic warming on the carbon balance of the moss, *CCG* was also calculated for temperatures of t + 3°C and t + 5°C.

Figure 6a shows the *CCG* of Colony A calculated for temperatures recorded at the field (t°C), and under two warming conditions (t + 3°C and t + 5°C). Because the respiration rate at night exceeded the gross photosynthetic rate, *CCG* showed diurnal fluctuation. Under the

present temperature conditions (t), CCG tended to increase throughout the main growing season. CCG at the end of the period (31 January 1991) was estimated to be 73.0 mg CO_2 g^{-1}.

The warming of $+3°C$ caused a slight decline in CCG at the end of the period, CCG was 60.0 mg CO_2 g^{-1}, about 82% of the value at the present temperature.

By contrast, the effect of further warming was quite remarkable. At $t + 5°C$, CCG tended to increase for about 20 days, but stopped increasing thereafter, because of low PPFD (cf. Fig. 1a). CCG at $t + 5°C$ at the end of the period was calculated to be 27.3 mg CO_2 g^{-1}, only 37% of the CCG at the present temperature.

When P_n (10) and R(10) of Colony B (Table 3) were used in the same calculation, CCG was highest at $t + 3°C$, although the effect of the warming was relatively small (Fig. 6b).

Discussion

Environmental factors affecting the photosynthesis and R rates

P_n values of *Sanionia uncinata* determined in this study are within the range summarized by Longton (1988) for polar bryophytes. However, the rates differed widely between colonies: the P_n and P_n/R ratio of Colony A was much smaller than those of Colony B throughout the growing season. Because the R rates of the two colonies did not differ significantly, the difference in net photosynthetic rate between the two colonies was largely due to the difference in gross photosynthetic rate.

The cause(s) of the low photosynthetic capacity of Colony A is not clear. Various stress factors, including desiccation, high light intensity, and a freeze–thaw cycle, are known to reduce the photosynthetic capacity of bryophytes (e.g., Kennedy 1993; Murray et al. 1993; Davey 1997). Davey (1997), who examined the effects of dehydration on carbon exchange in 14 Antarctic bryophytes, reported that dehydration led to a reduction in the photosynthetic rate and that the loss in the rate increased with the length of the dehydration period. The result shown in Fig. 5 indicates that desiccation can be a limiting factor of moss production in this area. However, it is unlikely that desiccation caused the reduction in photosynthetic capacity of Colony A; the water content of Colony A was near to or within the optimum range of water content for P_n for most of the growing season (Table 1; Fig. 4). In addition, from January to early February, water content of colony A was higher than that of Colony B (Table 1).

High light intensity may account for the between-colony variation, since Colony A grew in a site more exposed than that of Colony B. Deleterious effects of high light intensity on photosynthesis have been reported for several moss species (Oechel and Sveinbjörnsson 1978; Kappen et al. 1989; Murray et al. 1993). A marked inhibition of photosynthesis at light intensities higher than 800 µmol m^{-2}s^{-1} PPFD was reported for *Pogonatum alpinum* (Hedw.) Röhl. in the Alaskan arctic tundra (Oechel and Sveinbjörnsson 1978). Murray et al. (1993) reported that the 2-day treatment of high light intensity (800 µmol m^{-2}s^{-1} PPFD) caused a significant decline in the photosynthetic capacity of *Sphagnum* moss species. By contrast, Davey and Rothery (1997) found no indication of photoinhibition of photosynthesis in 14 Antarctic bryophytes at 700 µmol m^{-2}s^{-1} PPFD. They suggested that photoinhibition was not a significant factor in reducing productivity on most days during the growing season in the maritime Antarctic. However, as the maximum PPFD during the summer season exceeded 1500 µmol m^{-2}s^{-1} on King George Island, it seems possible that excessive irradiance had some deleterious effects on the photosynthesis of moss colonies in exposed sites. The data of irradiance over Colony B was not available. However, since Colony B grew on the partially shaded site (southwest-facing side of the rock) and was covered with snow until the middle of December, it is assumed that Colony B was rarely exposed to full ambient irradiance.

Freezing temperature may also be responsible for the low photosynthetic activity of Colony A. Kennedy (1993), who examined the effect of low temperatures on the photosynthesis of the Antarctic moss *Polytrichum alpestre* Hoppe., suggested that sub-zero temperatures and freeze–thaw stress may act as limiting factors to species viability and distribution, particularly when the insulating effect of snow cover is small. However, it seems unlikely that moss colonies growing on King George Island experience significant low temperature stress during summer. The minimum moss temperature rarely dropped below $-1°C$ in the 1990–1991 summer season (Fig. 1b). On the other hand, from May to November when minimum air temperature fell below $-4°C$ (e.g., Schroeter et al. 1995), the effect of freezing temperatures might be significant. Davey et al. (1992) reported that the main winter freeze in plant habitats occurred from May to November on Signy Island in the maritime Antarctic. It is assumed that Colony A was exposed to low ambient temperatures in spring because it was free of snow from at least the end of November. In contrast, it is unlikely that Colony B experienced significant low-temperature stress because of the prolonged snow cover. It is well known that snow cover acts as a thermal blanket, protecting the underlying habitats from the effects of declining air temperatures (e.g., Davey et al. 1992).

Sanionia uncinata in this study area showed a broad optimum range of temperatures for P_n. Similar broad optimum temperature ranges for P_n have been reported for other polar bryophytes (Oechel and Sveinbjörnsson 1978; Davey and Rothery 1997), although Collins (1977) and Davey and Rothery (1997) reported higher optimum temperature ranges for P_n of *S. uncinata* (15°–20°C). Conversely, R rate was strongly affected by temperature with the Q_{10} value of 2.1. This value is similar to the respiration Q_{10} reported for the same species from dry sites on Signy Island (Davey and Rothery 1997).

The impact of climatic warming on the carbon balance

Under present temperature conditions, the *CCG* of Colony A, calculated for the main part of the growing season (from 21 December 1990 to 31 January 1991), was 73.0 mg CO_2 g^{-1}. This *CCG* can be converted to the dry matter production per square meter of the moss colony using the average biomass (448 gdw m^{-2}) and the conversion ratio of 0.61 CO_2 to organic substances ($C_6H_{10}O_5$). The dry matter production of Colony A in this period was calculated to be 20 g m^{-2}. This value is much smaller than the dry matter production of *S. uncinata* on Signy Island (approximately 400 g m^{-2}; Collins 1977). Although the value of Colony A was calculated only for the main part of the growing season, the productivity of Colony A appeared to be very small.

In the simulation, the warming of +5°C caused a substantial (63%) decline in the *CCG* of Colony A, suggesting that climatic warming may cause a reduction of carbon gain in some Antarctic mosses. This conclusion is in contrast with the study of Davey and Rothery (1997), who suggested that a simple increase in temperature would lead to an increase in the rates of gross photosynthesis and respiration of Antarctic bryophytes, which in turn would cause an increase in their total productivity. This inconsistency is probably due to the small P_n/R ratio of the colony examined in the present study (Colony A). In fact, the effect of warming on carbon gain was much smaller when P_n (10) and $R(10)$ of Colony B (Table 3) were used in the same calculation (Fig. 6b).

If moss colonies with small P_n/R ratios, such as Colony A, are common in this region, climatic warming would have a significant effect on the terrestrial ecosystem. For example, replacement of one moss species with another, a phenomenon commonly observed in maritime Antarctic islands (Collins 1976; Nakatsubo and Ohtani 1992), would be accelerated. The number of colonies examined in this study is too small to determine whether a small P_n/R ratio is a common feature of mosses in this region. Net photosynthetic rates of Colony A were much smaller than those reported for *S. uncinata* on Signy Island (Collins 1977; Davey and Rothery 1997). However, the net photosynthetic rate of *S. uncinata* on Signy Island determined by Convey (1994) was small compared with the *R* rate (P_n/R = 0.55; calculated from Convey 1994, Fig. 3). Moreover, among the 14 moss species examined by Convey (1994), 11 species showed P_n/R ratios smaller than 1 (calculated from Convey 1994, Fig. 3). Although Convey's data were obtained at higher temperatures (13.1°–18.1°C) and a lower PPFD (225 μmol m^{-2} s^{-1}) than in this study, it seems that the small P_n/R ratio observed in this study is not an exceptional case in the maritime Antarctic.

There is some evidence that the photosynthetic activity of mosses is more sensitive to stress (e.g., desiccation, freezing etc.) than the respiratory activity (e.g., Alpert and Oechel 1985; Kennedy 1993). Therefore, it is expected that moss colonies growing in stressful habitats tend to show lower P_n/R ratios and that their carbon balance is more susceptible to climatic warming than those in favorable habitats. It has been suggested that carbon balance largely limits the distribution of some moss species (Alpert and Oechel 1985). It may be hypothesized, therefore, that climatic warming will reduce the habitat range of the moss species. However, it is also possible that temperature acclimation of the moss partly compensates for the effect of climatic warming. Published studies on the temperature acclimation of *S. uncinata* are controversial: Davis and Harrisson (1981) reported that the P_n and *R* responses showed clear signs of temperature acclimation, whereas Collins (1977) found no evidence of acclimation.

In this study, another possible consequence of climatic warming, i.e., the increase in growth period, is not taken into consideration. It is not clear whether the increase in growth period can compensate for the increased respiratory loss. The result shown in Fig. 6a (Colony A at t + 5°C) suggests that an increased growth period may not necessarily increase the carbon gain, especially under low light conditions. In addition, when snow cover protects the underlying vegetation from environmental stresses, early snowmelt would have some negative effect on the vegetation.

Based on global model simulations, global average precipitation is projected to increase during the twenty-first century (IPCC 2001). It is likely that the increase in precipitation will result in an increase in the carbon gain of bryophytes, because water availability is one of the most important factors limiting the productivity of many terrestrial bryophytes (Dilks and Proctor 1979; Alpert and Oechel 1985; Nakatsubo et al. 1989). However, in the maritime Antarctic, including King George Island, there is abundant precipitation, even under contemporary climatic conditions. Therefore, the effect of increased precipitation on the carbon balance of bryophytes would be relatively small in this area compared with other regions having limited water availability.

In conclusion, there was a considerable difference in the photosynthetic capacity between colonies of *Sanionia uncinata* in this area. The impact of warming on the carbon gain of the moss also differs widely between colonies. Some colonies showed a small net photosynthetic rate compared with *R* throughout the growing season. Although the cumulative carbon balance of these colonies is positive under contemporary climatic conditions, warming could reduce the carbon gain. These results support the assumption that climatic change could exert a significant effect on the Antarctic terrestrial ecosystems.

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