Estimation of the annual primary production of the lichen *Cetrariella delisei* in a glacier foreland in the High Arctic, Ny-Ålesund, Svalbard

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The fruticose lichen *Cetrariella delisei* is among the dominant lichen species in the deglaciated High Arctic areas of Svalbard. As part of a study of carbon cycling in the High Arctic, we aimed to estimate the primary production of lichen in a deglaciated area in Ny-Ålesund, Svalbard (79° N), by examining the effects of abiotic factors on the net photosynthesis (*Pn*) and dark respiration (*R*) rates of *C. delisei*. Experiments were conducted in the snow-free season of 2000 using an open-flow gas exchange system with an infrared gas analyser. Positive photosynthetic activities were observed on rainy days or soon after rainfall when the thallus water content was high, whereas photosynthetic activities dropped below the detectable limit on clear days because of the low thallus water content. Under a sufficiently high thallus water content and close to light saturation, *Pn* was nearly constant over a wide temperature range of 4 - 20 °C, while *R* increased with increasing temperature. We constructed a model for estimating the net primary production (*NPP*) of lichen based on the relationships between abiotic factors and the CO_2 exchange rate. The mean, minimum and maximum *NPP* values in the snow-free season, estimated using meteorological data obtained from 1995–2003, were 5.1, 1.0 and 8.4 g dry wt. m^{-2} snow-free season^{-1}, respectively. These results suggest that *NPP* is highly variable and the contribution of lichen to carbon input is small compared with that of vascular plants and mosses in the study site.

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A significant temperature increase in Arctic terrestrial ecosystems was observed during the 20th century (IPCC 2001). Although a number of recent works based on solar activity have predicted a decline in temperature over the next few centuries (for example, Perry & Hsu 2000), the Intergovernmental Panel on Climate Change (IPCC; 2001) projected that the globally averaged surface temperature will increase by 1.4 to 5.8 °C from 1990 to 2100, and this is expected to be most pronounced in high northern latitudes. Moreover, it has also been shown that temperature increases give rise to changes in snow cover, vegetation and permafrost (Cornelissen et al. 2001; IPCC 2001; ACIA 2004). Since carbon cycling in Arctic terrestrial ecosystems might be temperature limited, these areas are likely to intensely suffer the direct and indirect effects of global warming (for example, Hobbie 1999).

Lichens play an important role in Arctic terrestrial ecosystems (Alexandrova 1970; Williams et al. 1978; Tenhunen et al. 1992), and those living on ground surfaces are an important interface controlling the transfer of energy and materials such as carbon, nutrients and water (Kershaw & Field 1975; Tenhunen et al. 1992). In addition, some lichens such as *Cetraria* and *Cladonia* spp. are the main forage of reindeer, especially in winter (Boertje 1984; Chernov 1985; Cooper & Wookey 2001).

Understanding lichen production and/or growth rates is important in clarifying the role of lichen in Arctic and Antarctic ecosystems. A number of methods have been applied to studies of long-term production, such as direct (Lange 2000; Schroeter et al. 2000) and indirect measurements (Kappen et al. 1991; Friedmann et al. 1993). Using indirect measurements, the long-term production of lichens was recently estimated using a three-dimensional surface plot determined by measuring CO_2 exchange in the laboratory or directly at the study site (Kappen 1993, 2000; Schroeter et al. 1993; Schlensog et al. 1997; Green et al. 1999).

Models and direct measurement techniques for examining long-term variations in lichen production have also been developed (Kappen et al. 1991; Friedmann et al. 1993; Schroeter et al. 1995; Lange 2000). For example, Friedmann et al. (1993) constructed a straightforward simulation model of CO_2 exchange for Antarctic cryptoendolithic microorganisms and estimated their annual gross production and net photosynthetic gain over three years. Their results indicate that annual gross production and net photosynthetic gain vary widely between years. In polar ecosystems, where temperatures and precipitation are highly variable within and between years, the annual production of poikilohydric plants might also vary widely from year to year (for example, Schroeter et al. 2000; Uchida et al. 2002). Long-term monitoring and/or estimations are therefore needed to understand lichen production in polar ecosystems.

As part of a study on carbon cycling in a glacier foreland in Ny-Ålesund, Svalbard (see also Nakatsubo et al. 1998; Muraoka et al. 2002), we examined the effects of abiotic factors on the net photosynthesis (*Pn*) and dark respiration (*R*) rates of the dominant fruticose lichen *Cetrariella delisei* (Bory ex Schaer.) Kärnefelt and Thell (= *Cetraria delisei* (Bory ex Schaerer) Nyl.). We also constructed a model for estimating lichen production based on meteorological data. Using this model, the yearly variation in the net primary production of lichen was estimated for the past nine years (1995–2003), and the impact of climatic warming on the carbon balance of lichen was examined.

Materials and methods

Study site

The study was located in the glacier foreland of Austre Brøggerbreen (East Brøgger Glacier; 79° N, 12° E), 2 km south-west of Ny-Ålesund, Svalbard. From 1995 to 1998, the mean annual air temperature was –5.5 °C and the amount of precipitation was 362 mm in this area. Four permanent plots (sites 1, 2, 3 and 4) were established in 1994 along the primary successional series of the deglaciated area (Nakatsubo et al. 1998; Kume et al. 1999). Lichen thalli were collected from sites 3 and 4, which represent the later stage of succession. Site 3 was characterized by a patterned ground composed of small high-centred polygons. A mixed community of bryophytes and vascular plants (Mv) covered the marginal part of these polygons, whereas the central part consisted of almost bare ground (Bg). Site 4 was similar to site 3 except that black biological crust and lichens (Cl) covered the entire central part of the polygons. At site 3, the percent coverage of Mv, Cl and Bg was 53, 30 and 17 %, respectively, while at site 4 the coverage of Mv and Cl was 45 and 55 %, respectively (Nakatsubo et al. 1998). The dominant moss and vascular plant species at the sites were *Sanionia uncinata* (Hedw.) Loeske and *Salix polaris* Wahlenb, respectively. The dominant lichen was *C. delisei*, which consists of an irregular branched thallus and often forms small cushions (Sommerkorn 2000).

Gas exchange measurements

For gas exchange measurements, pure stands of *C. delisei* ($\phi = 6.5$ cm) were collected from colonies almost every day from 27 July to 12 August 2000. Three thalli were used per measurement; after the lower black portions were discarded the remaining portions (about 10 mm thick) were placed in a covered plastic dish in the field. Samples were brought to the nearby laboratory and weighed to determine the in situ water content.

CO_2 exchange was measured in the laboratory using an open-flow gas exchange system with an infrared gas analyzer (IRGA) (LI-6252, Li-Cor, NE, USA). A detailed description of this system and the IRGA calibration method are described in Uchida et al. (2002).

The plastic dishes holding the samples were enclosed in a cylindrical chamber (ϕ = 7.0 cm, height = 3.5 cm) into which a thermo couple sensor was inserted to monitor thallus temperature. The chamber was submerged in water to maintain a constant thallus temperature within an accuracy of ±0.2 °C. Ambient air containing about 365 - 380 ppmv CO_2 was introduced into the system at a rate of 300 ml min^{-1} and a light source was supplied in the form of a 700 W metal halide lamp (M700LS/BU, Iwasakidenki, Tokyo). Unless otherwise noted, the temperature in the chamber and photosynthetic photon flux density (PPFD) were controlled to 12 ± 0.2 °C and 800 ± 30 µmol photons m^{-2} s^{-1}, respectively.

The effect of thallus water content on *Pn* and *R* were determined by examining *Pn* and *R* rates with drying over a period of about 10 hours. Two moistened thallus samples were collected after rainfall and wetted with distilled water to produce the maximum water content. They were then kept in petri dishes for six hours prior to the gas exchange measurements to allow adaptation and to avoid possible resaturation respiration (Smith & Molesworth 1973). After obtaining the CO_2 exchange rate measurements, the samples were taken out of the chamber and weighed to obtain their fresh weights. They were then air-dried for 10 min to 2 h at which point a second CO_2 exchange rate was determined. These procedures were repeated until the *Pn* and *R* rates dropped below the detection limit of the IRGA. After completing the gas exchange measurements, the samples were dried to a constant weight at 80 °C to obtain their dry weights. The water content (%) of the samples was expressed as follows:

$$\text{water content (\%)} = ((\text{fresh wt} - \text{dry wt}) / \text{dry wt}) \times 100$$

The high water content determined in this study included not only the water contained in the thallus tissue but also the water adhering to the tissue.

To study the effect of temperature and light incidence on *Pn* and *R*, six samples were collected and optimally hydrated with distilled water to maintain high *Pn* activity. They were then kept in petri dishes for six hours before analysis. Three samples were used for measurement of the light–*Pn* curve and the remaining three samples were used for investigation of the temperature–*Pn* and temperature–*R* curves.

To examine the relationship between PPFD (0 - 800 µmol photons m^{-2} s^{-1}) and *Pn*, the incident PPFD in the chamber was reduced using translucent polyethylene sheets or black screens. Triplicate samples were illuminated at each level of PPFD for at least 3 min before measuring *Pn*. To determine the temperature dependencies of *Pn* and *R*, the temperature in the chamber was decreased from 20 to 4 °C at 3 - 5 °C intervals. Thallus temperature was controlled by changing the temperature in the water bath. About 5 - 6 h were required to obtain the temperature–*Pn* and temperature–*R* curves.

Carbon concentration

Five live thallus portions (about 7 mm thick) were collected from site 3 in August 2003. They were then air-dried prior to being transported to Japan for carbon concentration measurements using a CN-Analyzer (Yanaco MT-5, Yanagimoto Co. Ltd, Kyoto).

Climatic data

During the snow-free season of 2000 (from 4 July to 20 August), thallus temperature, PPFD and radiation were recorded at site 3. Hourly thallus temperatures (at about 5 mm deep) were measured using a data logger with a thermocouple sensor (L822, Unipulse Inc., Tokyo). At the same time, PPFD was measured at 10 minute intervals using a data logger (Kadec-UP, KONA System, Sapporo, Japan) with a quantum sensor (Li-190SA, Li-Cor). From 7 to 19 August 2000, global solar radiation was also recorded at 10 minute intervals using a data logger with a radiation sensor (PCM-01, PREDE, Tokyo). Climatic data (hourly mean values of minute by minute global radiation data and precipitation per every 12 hours) in Ny-Ålesund from 1995 to 2003 were provided by the Alfred Wegener Institute, Potsdam, Germany, and the Norwegian Meteorological Institute.

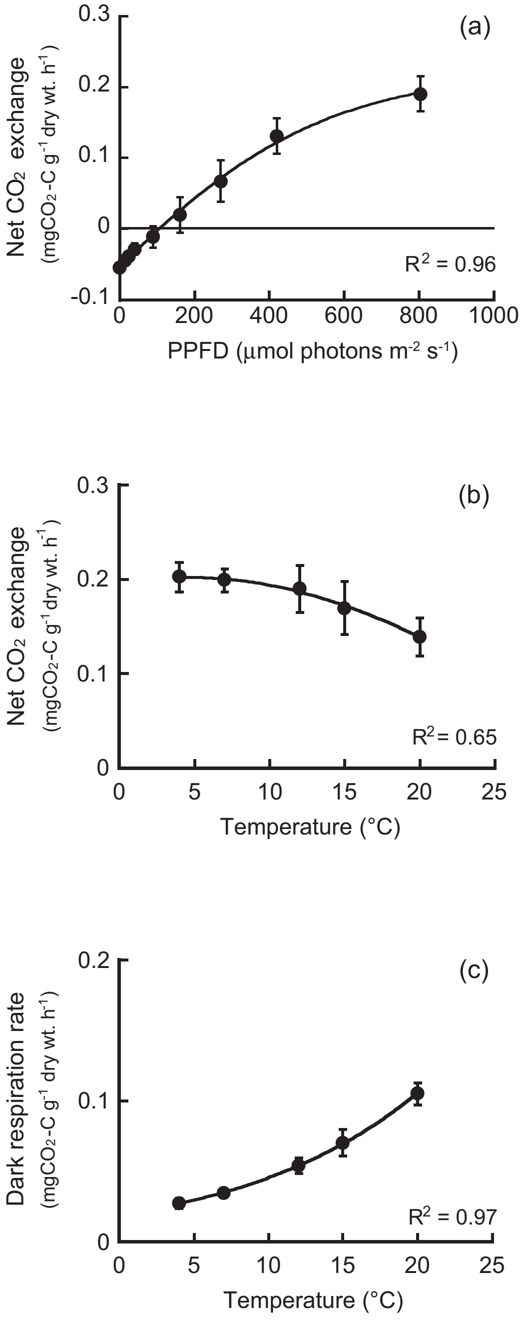

Fig. 1. Effect of light on the net photosynthetic (*Pn*) rate and temperature on the net photosynthetic (*Pn*) and dark respiration (*R*) rates of *Cetrariella delisei*. (a) Light–*Pn* curve. Temperature: 12±0.2 °C; water content: 270±30%. (b) Temperature–*Pn* curve. PPFD: 800±30 μmol photons m^{-2} s^{-1}; water content: 358±17%. (c) Temperature–*R* curve. Water content: 358±17%. Values represent the mean of three samples plus the standard deviation (SD).

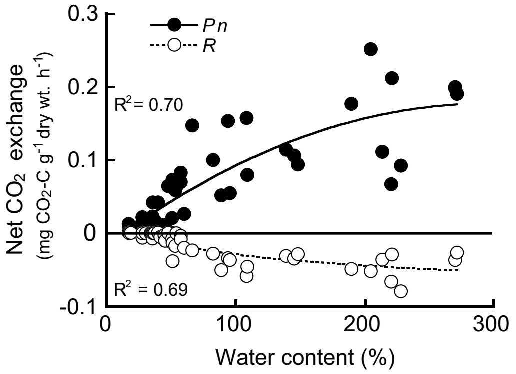

Fig. 2. Effect of water content on the net photosynthetic (*Pn*) and dark respiration (*R*) rates of *Cetrariella delisei* measured at the field water content (n=45). Temperature: 12±0.2 °C; PPFD: 800±30 μmol photons m^{-2} s^{-1}.

Estimation of net primary production of C. delisei

The net primary production (NPP_{wt}) of *C. delisei* was estimated from photosynthetic and respiration characteristics (Figs. 1, 2), biomass, PPFD and vegetation temperature according to Uchida et al. 2002. The basic assumption of the model is that the photosynthetic and dark respiration rates in the field are primarily dependent on the water content and secondarily on the temperature and PPFD.

The net photosynthetic rate at w% of thallus water content under 12 °C and 800 μmol photons m^{-2} s^{-1} ($Pn_{(w)}$) was given by the following formula, which was derived from the data shown in Fig. 2:

$$Pn_{(w)} = -2.21 \times 10^{-6} w^2 + 1.31 \times 10^{-3} w - 0.0167 \tag{1}$$

The dark respiration rate at w% under 12 °C ($R_{(w)}$) was given by the following:

$$R_{(w)} = -7.31 \times 10^{-2} + 5.08 \times 10^{-2} \times \log(w) \tag{2}$$

The net photosynthetic rate at w% of thallus water content, temperature t (°C) and 800 μmol photons m^{-2} s^{-1} ($Pn_{(w,\ t)}$) was expressed as follows:

$$Pn_{(w,\ t)} = Pn_{(w)}(\mathrm{a}t^2 + \mathrm{b}t + \mathrm{c}) \tag{3}$$

where a, b and c are coefficients of the temperature–*Pn* curve (Fig. 1b) (–0.0013, 0.0114 and 1.0401, respectively).

The dark respiration rate at t (°C) and w% of thallus water content ($R_{(w,\,t)}$) was expressed as follows:

$$R_{(w,\,t)} = R_{(w)}\mathrm{Q}_{10}{}^{(t-12)/10} \tag{4}$$

The Q_{10} value calculated from the temperature–R curve (Fig. 1c) was 2.3.

The effect of PPFD on the photosynthetic rate was calculated according to Thornley (1976):

$$Pg_{(w,\,t,\,i)} = \frac{\alpha i + P_{\max} - \{(\alpha i + P_{\max})^2 - 4\theta\alpha i P_{\max}\}^{0.5}}{2\theta} \times Pg_{(w,\,t)} \tag{5}$$

$$Pn_{(w,\,t,\,i)} = Pg_{(w,\,t,\,i)} - R_{(w,\,t)}, \tag{6}$$

where $Pn_{(w,\,t,\,i)}$ (mgCO$_2$–C m^{-2} h^{-1}) is the net photosynthetic rate at w% of thallus water content, t (°C) and i µmol photons m^{-2} s^{-1}; $Pg_{(w,\,t,\,i)}$ is the gross photosynthetic rate at w% of thallus water content, t (°C) and i µmol photons m^{-2} s^{-1} ; α is the initial slope of the PPFD–Pg curve; $P_{\max}$ is the asymptotic value of Pg at light saturation; θ is a dimensionless constant (0.8); t is the hourly thallus temperature; and i is the hourly PPFD in the field. To determine α and $P_{\max}$, the relationship between PPFD and Pn was recalculated from the relationship between PPFD and relative Pg. Equation (5) was then fitted to the relationship and α and P_{max} were determined as 0.0021 and 1.29, respectively.

Daily net production was expressed by the following:

$$NPP_{wt} = \Sigma Pn_{(w,\,t,\,i)} = \Sigma\,(Pg_{(w,\,t,\,i)} - R_{(w,\,t)}) \tag{7}$$

To estimate the NPP_{wt} of the past nine years (1995–2003), thallus temperature, PPFD, and thallus water content were estimated from the meteorological records of Ny-Ålesund according to Uchida et al. (2002). The relationships between radiation and thallus temperature, radiation and PPFD, and precipitation and thallus water content were calculated mainly from data of the snow-free season of 2000. These relationships were expressed as follows:

$$t = 0.0368R_{ad} + 3.928 \qquad R^2 = 0.62 \tag{8}$$

$$i = 2.197R_{ad} \qquad R^2 = 0.98 \tag{9}$$

$$\begin{array}{ll} P_r > 8.1 & w = 358 \\ 8.1 \geq P_r \geq 0.1 & w = 333.7\log(P_r\!+\!1) + 37.6 \\ & R^2 = 0.66 \\ P_r < 0.1 & P_n = R = 0 \end{array} \tag{10}$$

where R_{ad} is the global radiation and P_r is the precipitation per 12 h. In this study, we assumed that the maximum water holding capacity of the thallus (358%) was derived when P_r was in excess of 8.1 mm (Eq. 10). On the other hand, the rates of Pn and R were assumed to be zero when no significant precipitation was observed.

NPP_{wt} in the snow-free season, which started on the first rainy day of that season and ended on the first snowy day in late August or September, was calculated using equations (1)–(10) and the meteorological records from 1995 to 2003. To compare the obtained result with those of previous studies, the calculated NPP_{wt} (mgCO$_2$–C g^{-1} dry wt. season^{-1}) was converted to dry matter production per area using the carbon concentration (44.4%) and biomass of a pure community of standing *C. delisei* in this area (95 g dry wt. m^{-2}).

Effects of changes in temperature on net primary production

To clarify the effects of increasing temperature on lichen production, we estimated the potential production of *C. delisei* during the snow-free season. We assumed that the growing season does not change because it is difficult to estimate the exact timing and period of thawing. The temperature increase in the model was established as +3 to +6 °C.

Results and discussion

Effects of abiotic factors on photosynthesis and respiration

At a constant temperature (12 °C), the thallus photosynthetic response to light incidence exhibited saturation (Fig. 1a). The light compensation point occurred at about 120 µmol photons m^{-2} s^{-1} and light saturation appeared at over 800 µmol photons m^{-2} s^{-1}. These values are similar to, or somewhat higher, than those previously reported for Arctic and Antarctic fruticose lichens in open habitats (Kappen 1983; Ino 1985; Schipperges 1992).

The response curve of Pn to lichen temperature was typically broad, and Pn decreased gradually with increasing temperature in a temperature range of 4 to 20 °C (Fig. 1b). The optimal

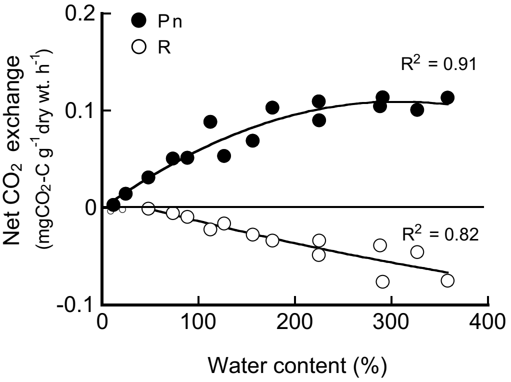

Fig. 3. Net photosynthetic (*Pn*) and dark respiration (*R*) rates of *Cetrariella delisei* at different water contents. The thallus was fully saturated then *Pn* and water content were measured as the tissue desiccated. Temperature: 12±0.2 °C; PPFD: 800±30 µmol photons m^{-2} s^{-1}.

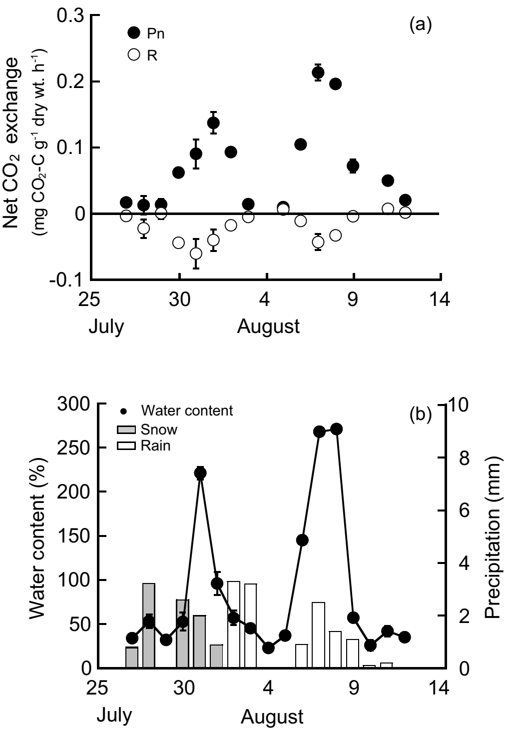

Fig. 4. (a) Net photosynthetic (*Pn*) and dark respiration (*R*) rates of *Cetrariella delisei* at the field water content. Temperature: 12±0.2 °C; PPFD: 800±30 µmol photons m^{-2} s^{-1}. Values represent the mean of three samples plus the SD. (b) Changes in thallus water content (at a depth of about 7 mm) in the colony of *Cetrariella delisei*. Values represent the mean of three samples plus the SD.

temperature for net photosynthesis was estimated as ≤4°C. Sommerkorn (2000) reported that the optimum temperature for net photosynthesis of *C. delisei* at 500 µmol photons m^{-2} s^{-1}, 350 ppm CO_2, is 12 °C. A similar optimum temperature was reported for other fruticose lichens (e.g. Kappen et al. 1995; Schroeter et al. 1995; Sommerkorn 2000). On the other hand, a low temperature optimum was previously reported for *C. delisei* and *C. nivalis* (Schipperges 1992), *Neuropogon acromelanos* (Kappen 1993) and *Usnea* and *Umbilicaria* spp. (Ino 1985). Kappen (1983) indicated that physiological activity differs between light and shade forms, even within the same lichen species. Some lichen species might alter their physiological activity under different environmental conditions.

The *R* of *C. delisei* increased with temperature up to 20 °C (Fig. 1c), and the Q_{10} value, which describes the proportional changes in rates with 10 °C changes in temperature, of *R* was 2.3 (n = 3). Although the *Pn* of *C. delisei* dropped below the detectable limit at a thallus water content of 25 %, it increased rapidly from a water content of 25 to about 100 %. The maximum *Pn* was maintained at a water content of about 300 % (Fig. 3), which is similar to the optimum water content of other lichens from cold regions (MacFarlane & Kershaw 1980; Smith & Gremmen 2001). On the other hand, *R* increased gradually with increasing thallus water content.

The potential rates of net photosynthesis (Pn_{pot}) and dark respiration (R_{pot}), which were determined from the field water content under constant temperature and light conditions (12 °C and 800±30 µmol photons m^{-2} s^{-1}), showed the importance of rainfall on physiological activity (Fig. 4a). Pn_{pot} and R_{pot} were relatively high on rainy days when the thallus water content was usually within a range of 50 to 270 % (Fig. 4b), whereas they were relatively low on snowy days (from 27 July to 1 August).

A higher thallus water content under snow was previously shown for *C. delisei* (Sommerkorn 2000) and *Usnea sphacelata* (Kappen 1993). It is suggested that lichens can take up water vapour from snow crystals that touch or surround the thallus (Kappen & Schroeter 1997). However, it has also been reported that thallus water content varies widely in the field on snowy days (Kappen & Breuer 1991). Although more than 3 mm rainfall was observed on 2 and 3 August, thallus water content was relatively low on these days (Fig. 4b). This is because the thalli were collected before rainfall or at least 12 h after rainfall.

Thallus water content decreased rapidly after rainfall resulting in a decrease in Pn_{pot}. When the thallus dried out, the Pn_{pot} dropped below the detectable limit of the IRGA. Figure 2 shows the relationship between Pn_{pot}, R_{pot} and water content in the field; the shape of the curve was similar to that obtained in the laboratory (Fig. 3). However, the Pn rates at the same water content were higher in the field (Fig. 2) than in the laboratory (Fig. 3). The reason for this is unclear, but one possible explanation is the difference in photosynthetic activity caused, for example, by feeding and/or the trampling effect of reindeer (Cooper et al. 2001; Cooper & Wookey 2001), acclimation and thallus shape.

Estimation of net primary production

To validate the model, we first estimated the daily NPP_{wt} in the growing season (27 July – 12 August 2000) using equations (1)–(6) and the data of thallus water content, PPFD and thallus temperature recorded in the field. The daily NPP_{wt} values ranged between 0.01 and 0.76 mgCO$_2$–C g^{-1} dry wt. day^{-1} (Fig. 5), which was much smaller than those of *Sanionia uncinata* in the same site (0.0 - 3.61 mgCO$_2$–C g^{-1} dry wt. day^{-1}; Uchida et al. 2002). The total NPP_{wt} for the study period (27 July to 12 August) was estimated as 15.4 mgCO$_2$–C g^{-1} dry wt. This value was more than twice the NPP_{wt} value obtained from the daily Pn_{pot} and R_{pot} data in Fig. 4a using equation (3)–(6) and the microclimate data (6.4 mgCO$_2$–C g^{-1} dry wt.). One possible reason for this discrepancy might be differences in the relationship between the amount of snowfall and thallus water content and between rainfall and thallus water content. Kappen & Breuer (1991) reported that thallus water content varies greatly during and after snowfall, probably as a result of the unavailability of snow as a direct water source for lichens. When excluding the snowy period, the total NPP_{wt} for the study period (4.5 mgCO$_2$–C g^{-1} dry wt.) was not so different from the value obtained from the Pn_{pot} and R_{pot} data in Fig. 4a using equations (3)–(6) (3.4 mgCO$_2$–C g^{-1} dry wt.).

It was previously reported that the production of *C. delisei* incubated in the field on Brøggerhalvøya (the peninsula on which our own field sites were located) in 1999 was 6.2 % of the dry mass (Cooper & Wookey 2001). The percent increase in dry mass in 1999 estimated in our study was 5.3 % (NPP: 5.0 g m^{-2} / biomass 95 g m^{-2} × 100), which was slightly lower than the value obtained by Cooper & Wookey. The difference between their value and our estimation could be partly because we did not consider the effects of dew, fog, melting snow and accuracy of our model.

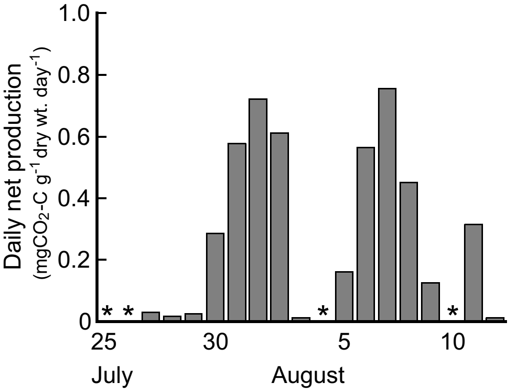

Fig. 5. Daily net primary production (*NPP*) of *Cetrariella delisei*. * No data.

In the Negev desert, dewfalls are frequent and are important for lichen production (Kappen et al. 1979). However, the effect of water uptake by dewfall might not be large on clear days in Ny-Ålesund. Diurnal courses of *C. delisei* thallus water content showed that it is maintained around 30 % (Schipperges 1992). We also observed that the relative humidity at a height of 15 cm from the soil surface rarely exceeded 90 % on clear days in 2002 (data not shown). On the other hand, the climate condition of Ny-Ålesund easily results in frequent fogs during summer (Lloyd 2001). In this study, the rain gauge sometimes detected fog as precipitation because of its high resolution (detectable limit: 0.1 mm). Since foggy days not detected by the rain gauge include just three days in 2001 and one day in 2002, the contribution of fog on lichen production could be small.

The accuracy of the model might also have contributed to differences in the production estimations. It is well known that interactions exist between changes in PPFD saturation and thallus water content, and changes in the optimum temperature and PPFD (Kappen et al. 1991; Lange 2000), but these were not considered in our model. A three-dimensional surface plot model

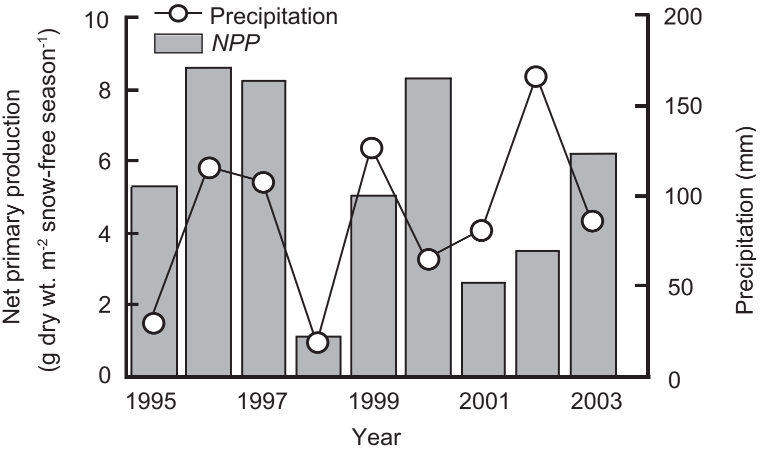

Fig. 6. Net primary production (*NPP*) of *Cetrariella delisei* and the amount of precipitation during the snow-free season.

would therefore be more accurate in estimating lichen production (e.g. Schlensog et al. 1997; Green et al. 1999; Kappen 2000). Furthermore, disturbances by reindeer might also have had an impact. Cooper & Wookey (2001) indicated that the growth rate of cut fruticose lichen thalli was lower than that of intact thalli. They used thalli collected from an enclosure not affected by reindeer grazing and trampling; however, we used thalli collected from areas that could have suffered from reindeer disturbances.

The snowy season is an important season for lichen production (Kappen 1993; Kappen et al. 1995). According to a photosynthetic activity value obtained by a laboratory measurement of thallus, production of *C. delisei* under a spring snow cover can be considerable (Sommerkorn 2000). However, continental Antarctic lichens under undisturbed snow were not active as measured by a portable PAM fluorescence system (Pannewitz et al. 2003). Although snow is one of the major water sources for the lichens, lichens might only become active for a brief time when the snow disappeared (Pannewitz et al. 2003). More field investigation is needed to reveal lichen production during the snow melting period.

Yearly variation and impact of climate warming on net primary production

The net primary production (*NPP*) of *C. delisei* calculated using the model showed high yearly variation (Fig. 6). The mean, minimum and maximum *NPP* values were 5.1, 1.0 and 8.3 g dry wt. m^{-2} snow-free season^{-1}, respectively. Several factors could have contributed to this variability. Uchida et al. (2002) suggested that poikilohydric moss production is limited by water availability because the lowest *NPP* they recorded in 1998 corresponded to a period of low precipitation during the snow-free season. On the other hand, the difference in *NPP* between 2001 and 2002 was small although the difference in precipitation between these two years was very large. One of the reasons for this difference could be rainfall intensity. Our model assumed that the maximal thallus water content is 358 % when precipitation is over 8.1 mm per 12 hours. Therefore, photosynthetic activity under a constant PPFD and temperature condition will be the same even if the amount of rainfall per 12 hours surpasses 8.1 mm. For example, on 21 July 2002, precipitation per 12 hours was 36 mm. Since the thallus water holding capacity is limited, the contribution of enhanced rainfall intensity on lichen production might not be so significant. Even with a constant water supply, temperature and light incidence would also influence lichen production (Uchida et al. 2002).

The annual net primary production of Arctic lichens reportedly ranges from 0.03 g m^{-2} for polar barrens on Cornwallis Island, Canada (Bliss et al. 1984), to <5 g m^{-2} for wet meadows in Demster and Eagle creeks in Alaska (Wein & Bliss 1974) (Table 1). The mean *NPP* value of *C. delisei* estimated in this study was similar to that of lichen communities on wet meadows in Demster and Eagle creeks (Wein & Bliss 1974). On the other hand, Lange (2000) collected the gelatinous cyanolichen *Collema cristatum* and incubated it in a quasi-natural habitat in the Botanical Garden in Würzburg, Germany, and estimated its

Table 1. Net annual production and phytomass of lichens in Arctic regions.

Location	Vegetation type	Net annual production ($g\ m^{-2}$)	Phytomass ($g\ m^{-2}$)	Reference
Demster, Alaska (64° N)	Wet meadow	<5	69	Wein & Bliss 1974
Eagle Creek, Alaska (65° N)	Wet meadow	<5	25	Wein & Bliss 1974
Stordalen, Sweden (68° N)	Wet meadow	<3	12	Rosswall et al. 1975
Cornwallis Island, Canada (74° N)	Polar barrens	0.03	2.9	Bliss et al. 1984
Devon Island, Canada (75° N)	Dwarf shrub heath	4	48	Bliss 1977
Devon Island, Canada (75° N)	Cushion plant–moss fellfield	3	49	Bliss 1977
Devon Island, Canada (75° N)	Cushion plant–moss fellfield	2	23	Bliss 1977
King Christian Island, Canada (77° N)	Moss–graminoid meadow	<1	10	Bliss & Svoboda 1984
Ellef Ringnes Island, Canada (78° N)	Grass heath	<1	29	Bliss & Svoboda 1984
Ellef Ringnes Island, Canada (78° N)	Grass heath	<1	9	Bliss & Svoboda 1984
Ny-Ålesund, Svalbard (79° N)	Cushion plant–moss heath	1.0 - 8.4	95	Present study

annual production as 25.8 $gC\ m^{-2}$, which is about five times higher than the average value estimated here.

Muraoka et al. (2002) and Uchida et al. (2002) reported that the *NPP* values of the vascular plant *Salix polaris* and the moss *Sanionia uncinata* at the same study site were 98 (the carbon concentration was assumed to be 50 % from van der Wal et al. 2000) and 17 g dry wt. m^{-2} snow-free $season^{-1}$, respectively. The *NPP* of lichen is much smaller than those of these two species. Although moss is also a poikilohydric plant, the average lichen production obtained here was about one-third that of moss production. This is partly due to the low photosynthetic activity of lichens.

Global warming is likely to be most intense at high latitudes. In this study, *C. delisei* showed a low optimum temperature for net photosynthesis, suggesting that temperature increases might reduce the carbon gain of lichen. To clarify the effects of increasing temperature on lichen production, we estimated the potential production of *C. delisei* during the snow-free season. In the simulation, although all estimated values showed positive production, a warming of + 6 °C caused a substantial decline in lichen production (Table 2). This is because although the temperature response of net photosynthesis is broad, respiration rates increased with increasing temperature in our model. Respiration therefore seems to be the main driver of *NPP* change with warming. The effect of temperature acclimation on lichen production should also be considered because respiration responses in Arctic and alpine plants show rapid acclimation (Körner 1999). Lange & Green (2005) reported that some soil-crust lichen species showed seasonal changes in the temperature sensitivity of dark respiration. However, Kershaw (1985) indicated that temperature acclimation differs between different populations. Although further research is needed to clarify this point, it is suggested that climate warming would cause a reduction in carbon gain in some Arctic lichens. On the other hand, it is also projected that global warming will cause not only a temperature increase but also a change in precipitation and the duration of snow cover. It has been predicted that global warming would cause increased rainfall in the Norwegian Arctic (Førland & Hanssen-Bauer 2000). Precipitation timing, duration and intensity would also impact lichen production (Lange 1980; Smith & Gremmen 2001), so future precipitation changes are also important to consider when predicting lichen production.

Table 2. Effect of temperature increase on the net primary production of *C. delisei*.

Year	% reduction of production	
	+3 °C	+6 °C
1995	12	27
1996	14	24
1997	15	37
1998	23	55
1999	24	55
2000	12	26
2001	29	67
2002	28	67
2003	17	40

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