Photosynthesis in a sub-Antarctic shore-zone lichen

V. R. Smith[1] and N. J. M. Gremmen[2]

[1]Department of Botany, University of Stellenbosch, Private BagXI, Matieland, 7602, South Africa; [2]Data Analyse Ecologie, Dwarsdrift 24, 7981 AP Diever, The Netherlands

Author for correspondence:
V. R. Smith
Tel: +27 21 8083111
Fax: +27 21 8083607
Email: vs2@akad.sun.ac.za

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Summary

• Photosynthetic responses to moisture, light, temperature, salinity and inorganic nitrogen fertilization are reported for a shore-zone lichen *Turgidiusculum complicatulum* (formerly *Mastodia tesselata*), a possible recent introduction to sub-Antarctic Marion Island.

• Optimum moisture contents for net photosynthesis were 225–346% (ash free, dry mass). Net CO_2 exchange was dominated by a strong temperature dependence of respiration rate. Net photosynthetic rate responded sharply to increasing PPFD and saturated below 300 μmol m^{-2} s^{-1}, but electron transport rate (ETR) increased up to approx. 900 μmol m^{-2} s^{-1} PPFD suggesting that gross photosynthesis responded to light to this level. Nonphotochemical fluorescence quenching increased rapidly with PPFD up to approx. 400 μmol m^{-2} s^{-1} and thereafter more slowly. Even at high PPFD (1050 μmol m^{-2} s^{-1}) most PSII centres were open.

• Salinity did not significantly influence CO_2 assimilation rate; however, NH_4NO_3 significantly depressed net photosynthesis rate at all salinities except 100% seawater. ETR and dark respiration rate were increased by NH_4NO_3.

• The response of *T. complicatulum* to light and temperature enables high rates of CO_2 assimilation under the island's microclimatic regime; if sufficiently hydrated, the lichen would exhibit near maximal photosynthesis rates for approx. 75% of the photoperiod over the year.

Key words: *Turgidiusculum complicatulum, Mastodia tesselata*, lichen photosynthesis, sub-Antarctic, salinity, moisture, temperature, light, inorganic nitrogen, chlorophyll fluorescence.

Introduction

Turgidiusculum complicatulum (Nyl.) Kohlm. et Kohlm. (formerly and still more commonly referred to as *Mastodia tesselata*) is a bipolar coastal lichen species with a dark green or brown-green to black foliose thallus up to 10 mm high. In the Arctic it occurs in eastern Siberia (Lamb, 1948; Lindsay, 1974). In the southern hemisphere subpolar region it is found in the Maritime Antarctic (Follman, 1965; Gremmen *et al.*, 1994), and from four sub-Antarctic islands; South Georgia Island (Lindsay, 1974), Bouvetøya (Jorgensen, 1986), Macquarie Island (Selkirk *et al.*, 1990) and Marion Island. It occurs mainly on rocky shores exposed to seaspray and even seawater inundation, suggesting that it might be a halophyte. It is also occasionally found at inland sites away from any obvious seawater influence (Engelskjøn, 1987). Both on the shore and inland, however, it is particularly abundant in areas affected by guano and has been considered a nitrophilous, or ornithocoprophilous species. The lichen's free-living phycobiont, *Prasiola crispa* (Lightf.) Menegh., certainly occurs most abundantly, and shows greatest vigour, at sites heavily influenced by guano, so much so that Schofield and Ahmadjian (1972) consider *P. crispa* to be 'one of the most nitrophilous organisms known' and 'strongly ornithocoprophilic wherever it is found'. They state that in polar regions the alga lichenizes where nitrogen levels are lower, but that *T. complicatulum* is still considered a 'well-known nitrophilous species'.

Quite possibly *T. complicatulum* is a recent introduction to Marion Island since it was first found there (by N. J. M. G.) only in 1993, even though several previous investigations were of the sort that might be expected to have discovered it were it present; these included the ecology of the shore-zone

(in which *Prasiola crispa* was recorded; De Villiers, 1976); water relations of shore-zone plants (Smith, 1978), a detailed phytosociological survey that paid particular attention to cryptogams (Gremmen, 1981), and three intensive lichen collecting efforts (Lindsay, 1976; H. Hertel, pers. com.). The lichen is locally abundant on some coastal cliffs, with a mean standing crop of up to 312 g m^{-2} (Gremmen *et al.*, 1995). It has not been found inland and is particularly abundant at nutrient-enriched sites, such as around cormorant nests, penguin rookeries and skua and gull perches. It has been chosen as an indicator shore-zone species in a research programme addressing climatic and biotic changes at the island (Smith, 1993a) and in this account we describe the lichen's photosynthetic (CO_2 assimilation and chlorophyll fluorescence) responses to moisture, light, temperature, salinity and inorganic nitrogen fertilization.

Materials and methods

T. complicatulum thalli were collected on the island's east coast and transported to the laboratory where they were picked clean of debris and rinsed with tap water (tapwater on the island has an almost identical chemical composition to the rainwater, being ultra-oligotrophic with undetectable levels of inorganic N and P; Grobbelaar, 1978). This process was generally completed within 1 h of collection. The thalli were placed in Petri dishes containing wet filter paper. Each Petri dish was covered with a larger one and put in a 60 l aquarium that had wet paper towels lining its base. The aquarium was placed outside, on the south side of the laboratory so that it was shielded from direct sunlight, which is quite rare at the island. A glass pane was placed on the top of the aquarium to keep out the strong wind and rain, both of which are very prevalent. Temperature and photosynthetic photon flux density (PPFD) in the aquarium were monitored with a thermistor and a quantum sensor (LI-COR Inc., Lincoln NE, USA), respectively, connected to a MCS 101 data logger (MC Systems, Cape Town, South Africa). Relative humidity in the aquarium, as indicated by a thin-film capacitance sensor connected to a KM 8001 digital meter (Kane-May Ltd, Swallowfield, Herts, UK) was always 100%; in the Petri dishes the atmosphere would certainly have been at, or very close to, saturation.

CO_2 assimilation rates of whole thalli were measured in an assimilation chamber connected to ADC Mark 3 infra red CO_2 and H_2O analysers (Analytical Development Company, Hoddesdon, UK) operating in differential mode in an open gas exchange system described by Smith (1988). The chamber was illuminated with a 400-W high pressure sodium lamp. PPFD in the chamber was measured with a LI-COR quantum sensor and chamber air temperature and thallus temperature measured with fine wire thermocouples.

The effect of thallus moisture content on assimilation rate was determined on six thalli which were soaked in water early in the morning and maintained for 24 h in Petri dishes containing wet filter paper, in the outside aquarium. Temperature and PPFD in the aquarium varied according to time of day and were different for the six samples, but were between 3.1°C and 11.1°C, and 0 and 234 μmol m^{-2} s^{-1}, respectively. The following morning the thalli were put on a plastic weighing boat and placed in the assimilation chamber. Thallus temperature was adjusted to 10°C or 15°C, PPFD to 130 μmol m^{-2} s^{-1} and water vapour pressure of the incoming air (measured with an infra red H_2O analyser) adjusted so that water vapour pressure deficit (VPD) in the chamber was zero (i.e. at the saturated value for the chamber air temperature). Once the differential CO_2 value had stabilised, VPD was increased to between 0.3 and 0.6 kPa so that the sample gradually dried out, and assimilation rate was measured continuously. At intervals (15–30 min) the sample, in its weighing boat, was removed from the chamber, quickly weighed and replaced. If necessary, VPD was adjusted to control the rate of thallus drying. In this manner the assimilation rate at between 20 and 30 thallus different moisture contents could be measured in 9–11 h.

The influence of light and temperature on CO_2 assimilation rate was determined on three thalli as follows. A freshly collected thallus was soaked in tapwater and excess water shaken off by hand. The thallus was then kept for 24 h in a Petri dish containing wet filter paper in the outside aquarium. During the 24 h, temperature was between 1.5 and 6.7°C, 3.2 and 8.2°C, and 3.1 and 10.7°C, and maximum PPFD was 154, 198 and 235 μmol m^{-2} s^{-1}, respectively, for the three thalli used. The following morning each thallus was weighed and placed in a darkened assimilation chamber and chamber temperature adjusted so that thallus temperature was 10 ± 0.1°C. The thallus was then subjected to increasing PPFD, from 0 to saturating levels (approx. 300 μmol m^{-2} s^{-1}; PPFD was not raised further to avoid photo-inhibiting the thallus). Thallus temperature was maintained at 10 ± 0.1°C throughout the light run. The thallus was then darkened and the temperature changed. After 30 min in the dark at the new temperature the A : PPFD response was tested again. In this way A : PPFD responses were obtained at 1, 5, 10, 15, 20 and 25°C for each thallus, the sequence of temperatures after the first 10°C curve being different for each thallus. During the assimilation measurements vapour pressure of the incoming air was either held at the saturated value for the particular leaf temperature or, where this lead to excessive condensation in the chamber (for instance, when maintaining low thallus temperature at high light intensity), it was adjusted so that there was only a slight film of condensation in the chamber. In this way it was possible to measure gas exchange over long periods without the thalli drying out to any appreciable extent; for two of the samples moisture content decreased (from 252% to 220% and from 284% to 268%) and for one sample it increased slightly (from 273% to 280%) between the start and end of the assimilation measurements.

The effect of salinity and inorganic nitrogen level on CO_2 assimilation rate was determined on freshly collected whole thalli, placed in glass Petri dishes filled with mixtures of sea water and tap water (0, 25, 50, 75 and 100% seawater), with or without added NH_4NO_3 (10 mg N l^{-1}). Thus, there were five salinity treatment and two inorganic nitrogen treatment levels, with four replicates of each. The island precipitation, freshwaters and soils are extremely nutrient poor; 10 ppm inorganic N is in the upper part of the range of concentrations found for freshwaters and precipitation influenced by volatilisation off penguin rookeries and seal wallows (Grobbelaar, 1978) and in the lower part of that found for water draining from such areas (Lindeboom, 1984). After 4 h the solutions were drained from the samples which were kept in their Petri dishes in the aquarium outside the laboratory for 19 d. Every second day the thalli were soaked for *c.* 5 min in fresh aliquots of the appropriate seawater/tapwater solution and the solution drained off. The thalli remained hydrated throughout the 19 d. Temperature and PPFD in the aquarium were not measured during this period. Before measuring CO_2 assimilation rate, the thalli were soaked briefly in the appropriate solution and excess moisture shaken off by hand. They were then placed in a preconditioning chamber (Smith, 1993b) with an air temperature of 10°C and 190 μmol m^{-2} s^{-1} PPFD for at least 60 min before being transferred to the assimilation chamber, where PPFD was also at 190 μmol m^{-2} s^{-1} and temperature close to 10°C. Temperature was adjusted so that thallus temperature was 10 ± 0.2°C and the differential CO_2 value measured when it stabilised (generally this occurred within 5 min).

The thallus sample was weighed after the assimilation rate measurements, oven-dried (60°C for 48 h), weighed, ashed (550°C, 24 h) and reweighed. All CO_2 assimilation rates reported here are on an ash-free dry mass basis.

Chlorophyll fluorescence was measured using a Hansatech FMS1 pulse-modulated fluorometer (Hansatech Instruments Ltd, Norfolk). A thallus was placed in the cap of a 35-mm slide film canister that fitted into the base of the (open) fibre-optic adapter supplied with the FMS1. The sample end of the fibre optic was fastened into the mounting collar of the adapter so that it pointed at the thallus surface. The fibre optic was kept in the same postion for all measurements throughout the study. The adapter containing the thallus and fibre optic was placed in a water-jacketted glass chamber. Air from outside the laboratory was passed at 100 ml min^{-1} through a short copper tube contained in the water jacket and then through the chamber. Air temperature was monitored with a fine wire thermocouple placed just above the thallus, to the side of the light beam from the fibre optic, and could be controlled by adjusting the temperature of the water flowing through the water jacket. Thallus temperature was not measured. The glass chamber was darkened by inverting a plastic bucket over it and covering the bucket with black cloth. After 30 min of dark adaptation the modulated light was turned on, the F_0 signal recorded and then a saturating pulse (approx. 4000 μmol m^{-2} s^{-1} PPFD, 0.8 s duration) applied to measure F_m. After 10 min in the dark the actinic light was switched on at a low intensity (15 μmol m^{-2} s^{-1} PPFD). After a further 10 min the fluorescence signal (F) was recorded, the saturating pulse reapplied and F'_m measured. The actinic light was switched off and far red light applied for 5 s during which the minimum fluorescence yield was recorded as F'_0. The actinic light was again switched on, at a higher PPFD than before, and after a further 10 min the F, F'_m and F'_0 measurements repeated. These fluorescence parameters were obtained for a range of PPFDs from 0 to 1050 μmol m^{-2} s^{-1}. They were used to calculate (relative) electron transport rate (ETR = PPFD × $(F'_m - F)/F'_m$), non-photochemical quenching ($q_N = (F_m - F'_m)/(F_m - F'_0)$) and the reduction state of PSII reaction centres ($Q_r/Q_t = (F - F'_0)/(F'_m - F'_0)$); Björkman & Demmig-Adams (1995).

Results

Influence of thallus moisture content on net CO_2 assimilation rates

Optimum moisture values for CO_2 assimilation were between 225 and 346% (ash-free, dry thallus mass basis) for the two temperatures tested (10 and 15°C; Fig. 1). Assimilation rates of fully saturated thalli were 36–58% of rates at optimum water content and increased gradually as the thalli dehydrated. Assimilation rate declined sharply below the optimum moisture content. On average, assimilation rate was within 10% of the maximum for moisture contents between 190% and 425%. Moisture contents of soaked thalli from which excess surface water was shaken off (i.e. the samples used to assess the effect of light/temperature) were well within this range, between 220 and 280%. For an unknown reason the thalli used to study the influence of seawater/nitrogen had lower moisture contents, between 162 and 214%.

Influence of light and temperature on net assimilation rates

Fig. 2 shows the response of net CO_2 assimilation to photosynthetic photon flux density at six temperatures. Dark respiration rate (intercept on *y* axis in the figure) increased markedly with temperature, from a mean of 1 μmol CO_2 g^{-1} h^{-1} at 1°C to 73 μmol g^{-1} h^{-1} at 25°C. Because of this large temperature-dependence of respiration, assimilation rates at low light (below *c.* 100 μmol m^{-2} s^{-1}) were inversely related to temperature. As PPFD increased above 100 μmol m^{-2} s^{-1}, the between-temperature differences in assimilation rate decreased, except at 25°C where rates were lower than those at lower temperatures across the whole range of light levels.

The curves in Fig. 2 were fitted using the rectangular hyperbola equation of Smith (1936), modified to include respiration as suggested by Lederman & Tett (1981):

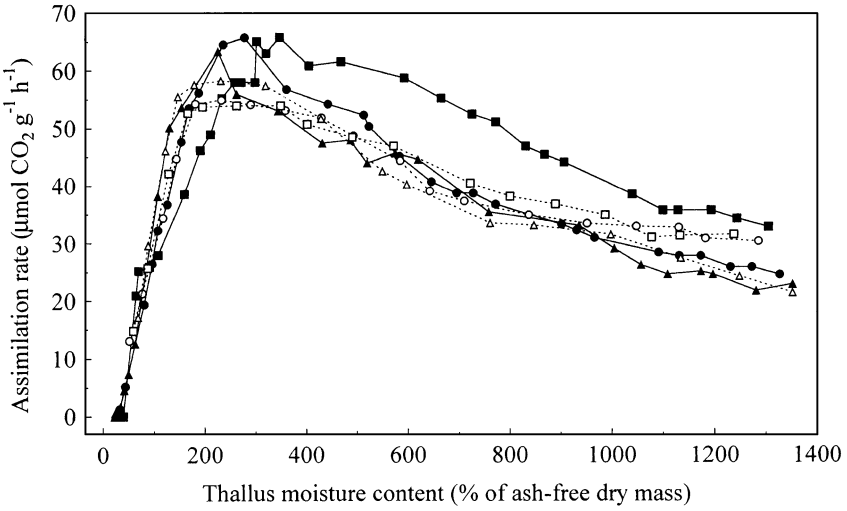

Fig. 1 Dependence in *Turgidiusculum complicatulum* of net CO_2 assimilation rate on moisture content at 130 μmol m^{-2} s^{-1} PPFD and 15°C (closed symbols, solid lines) or 10°C (open symbols dashed lines).

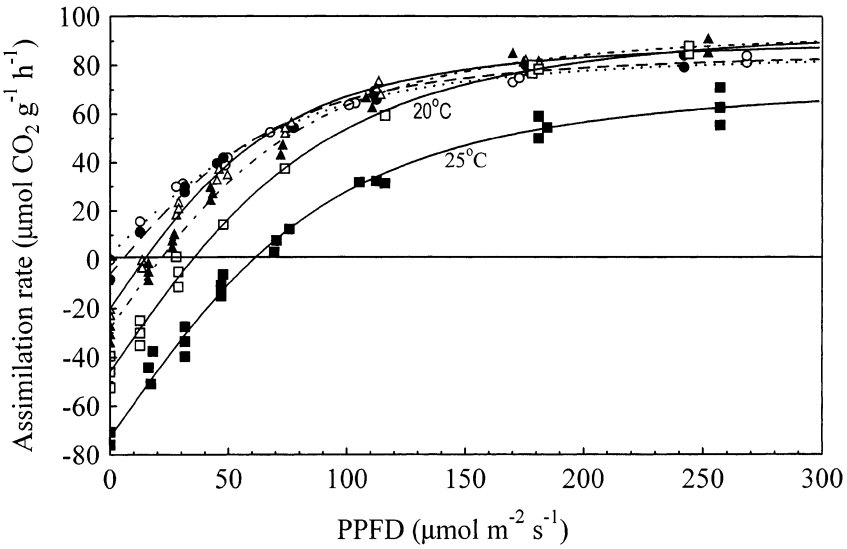

Fig. 2 Dependence in *Turgidiusculum complicatulum* of net CO_2 assimilation rate on PPFD at different temperatures. Each curve is the fit of eqn 1 to the combined data for three replicates. 1°C, open circles, dotted line; 5°C, closed circle, dashed line; 10°C, open triangle, solid line; 15°C, closed triangle, dotted-dashed line; 20°C, open squares, solid line; 25°C, closed squares, solid line.

$$A = Ag_{max}(\alpha I / (Ag_{max}^2 + (\alpha I)^2)^{1/2}) - R \qquad \text{Eqn 1}$$

(A, net CO_2 assimilation rate; Ag_{max}, maximum rate of gross photosynthesis; α, initial slope of the A : PPFD curve (the incident quantum yield, a measure of the maximum efficiency of photosynthesis); I, PPFD; and R, respiration rate (intercept of curve on ordinate axis in Fig. 2).)

This model explained > 99% of the light-induced variation in assimilation rate for individual replicates and 97–98% of the variation of the combined data for the three replicates. The equation coefficients were estimated for each of the 18 (6 temperatures × 3 replicates) A : PPFD response curves and used to calculate P_{max} (= Ag_{max} – R; the maximum light-saturated rate of net CO_2 assimilation), $I_k/2$ (= $Ag_{max}/2\alpha$; the PPFD value at the onset of light saturation for photosynthesis; Talling, 1957) and compensating PPFD (where net CO_2 assimilation is zero). Fig. 3 shows the influence of temperature on these parameters, and on incident quantum yield.

Light saturated maximum CO_2 assimilation rate increased with temperature between 5 and 20°C, but was much lower at 25°C than at all lower temperatures. Comparing P_{max} values in Fig. 3(a) with the curves in Fig. 2 it is evident that assimilation rate at the highest PPFD levels tested (250–270 μmol m^{-2} s^{-1}) was within 10% of the calculated maximum value for all temperatures. Incident quantum yield (Fig. 3b) increased sharply with temperature up to 10°C and stayed constant as temperature increased further. Compensating PPFD (Fig. 3c) increased

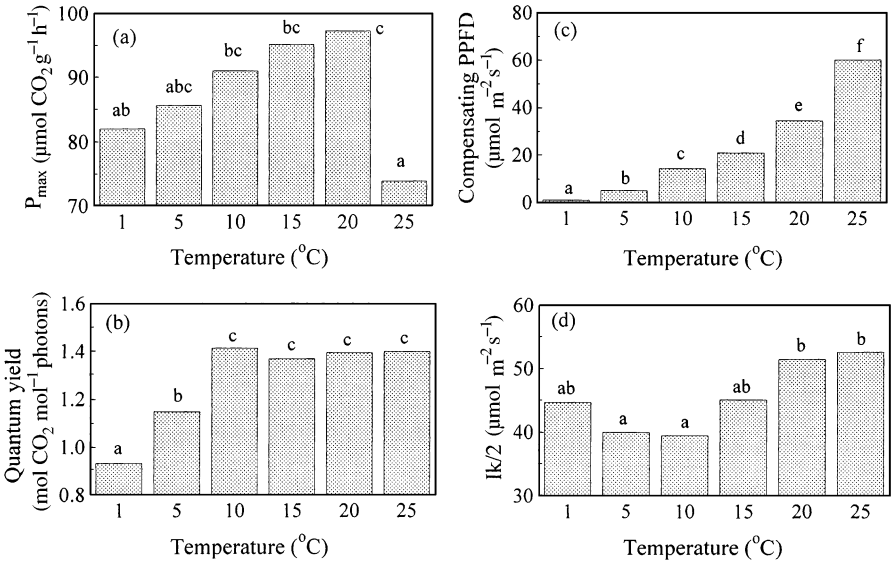

Fig. 3 Values of (a) P_{max} (b) incident quantum yield (c) compensating PPFD and (d) onset of light saturation, at different temperatures in *Turgidiusculum complicatulum*.

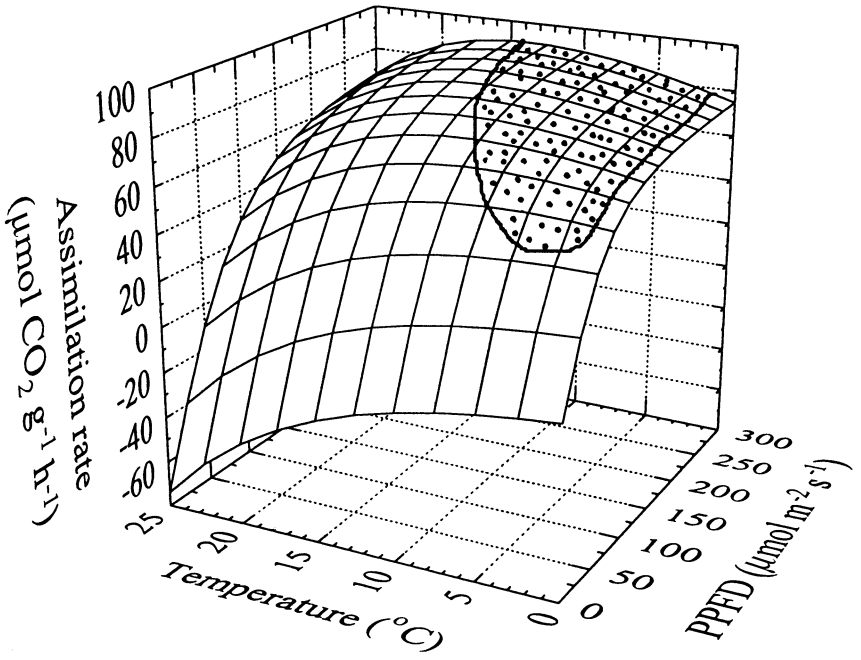

Fig. 4 Response surface of net CO_2 assimilation rate to PPFD and temperature. The stippled area indicates that part of the light/temperature matrix representative of 75% of daytime over the year.

exponentially with temperature, reflecting the marked temperature response of respiration and the consequent need for increasingly higher light levels to attain positive assimilation as temperature rises. The onset of light saturation (Fig. 3d) occurred at successively higher PPFD values as temperature increased from 10 to 25°C. However, even at 20 and 25°C Ik/2-values were low (30–60 μmol m^{-2} s^{-1}).

The temperature dependence of the three coefficients in equation 1 was examined. Simple linear regression explained 97% ($P < 0.001$) of the change in Ag_{max} with temperature. R was exponentially related to temperature ($r^2 = 0.98$, $P < 0.001$). The rectangular hyperbola equation of Burk & Lineweaver (1935) adequately ($r^2 = 0.88$; $P = 0.01$) described the α : temperature relationship:

$$\alpha = \alpha_{max}(T/(k + T)) \qquad \text{Eqn 2}$$

(T, temperature in °C; α_{max}, the maximum quantum yield; k, the half-saturation constant (temperature at which $\alpha = {}^1/_2\alpha_{max}$).)

These regression equations predicting the values of Ag_{max}, α and R at different temperatures were incorporated into eqn 1 to model the response of CO_2 assimilation to light and temperature (Fig. 4). The model explained 93% of the

variation in the assimilation rate data set for the three replicates across the range of temperature and PPFD levels tested. The response surface clearly shows that net CO_2 exchange in the lichen is overwhelming dominated by the strong temperature-dependence of respiration rate, so that CO_2 assimilation rate increases only slightly with increasing temperature at saturating PPFD, and decreases with temperature at low PPFD. Even at high light, increasing temperature above 20°C depressed photosynthetic rate.

ETR increased up to *c.* 900 μmol m^{-2} s^{-1} PPFD (Fig. 5a), suggesting that gross photosynthesis responded to light at least up to this level. Nonphotochemical fluorescence quenching increased rapidly with PPFD up to *c.* 400 μmol m^{-2} s^{-1} and then more slowly at higher light levels (Fig. 5b). Even at the highest PPFD tested (1050 μmol m^{-2} s^{-1}) the fraction of PSII centres that were in the closed state was only about 80% (Fig. 5c).

Influence of nitrogen and seawater on net CO_2 assimilation and chlorophyll fluorescence

Seawater, at concentrations up to 100% (i.e. pure seawater), did not significantly influence CO_2 assimilation rate after 19 d of treatment (Fig. 6). However, addition of NH_4NO_3 significantly depressed net CO_2 assimilation at all salinity levels except 100% seawater. Thallus moisture contents in this experiment (162–214%) were in the lower part, and just below, the range of optimal moisture contents for net photosynthesis and this might have complicated the comparison. However, including moisture content as covariate (using a 4th-order polynomial fit to the data in Fig. 1) made little difference to the analysis of variance results in Fig. 6 – inorganic N depressed CO_2 assimilation at all salinity levels except 100% seawater and, within N treatment, there was no significant difference in assimilation rate between the various salinity levels.

Dark respiration rate was not measured in this seawater/inorganic nitrogen trial but a subsequent experiment (data not shown) in which thalli were exposed for 10 d to freshwater or 100% seawater, both with or without 10 mg (NH_4 + NO_3)-N l^{-1}, showed that respiration rate (net CO_2 assimilation at 10°C and zero PPFD) was enhanced by N addition; by 20% in the freshwater treatment and by 13% in the seawater treatment (both $P < 0.01$; moisture content of the samples was between 209 and 238%). This suggests that elevated respiration, rather than a lowered gross photosynthesis, caused the decreased net photosynthesis rates of the thalli treated with inorganic N. Further evidence for this is the fact that, at both levels of salinity, electron transport rate measured by chlorophyll fluorescence was higher for the + N than for the zero N treatment ($P = 0.05$). Within N treatment, mean ETR of the thalli supplied with saltwater was not significantly different from that of thalli supplied with freshwater.

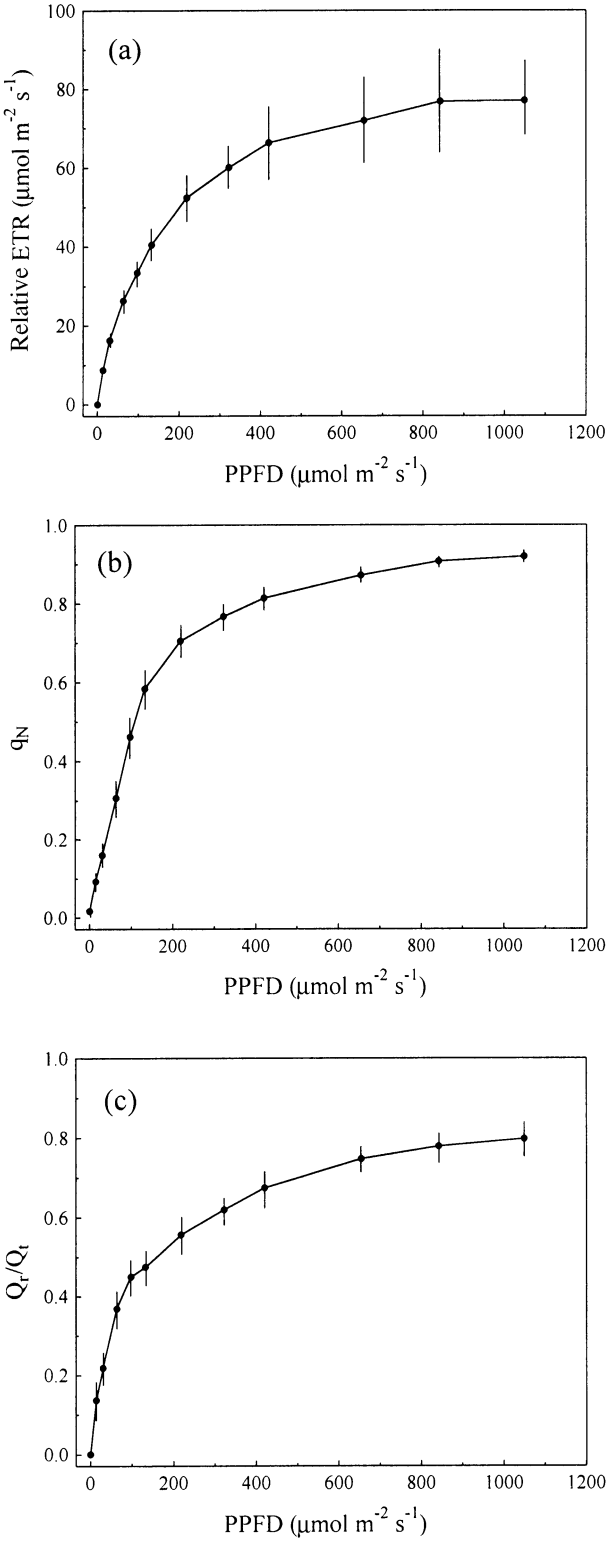

Fig. 5 Dependence on PPFD of (a) relative electron transport rate (b) nonphotochemical quenching and (c) the fraction of closed PSII centres in *Turgidiusculum complicatulum*.

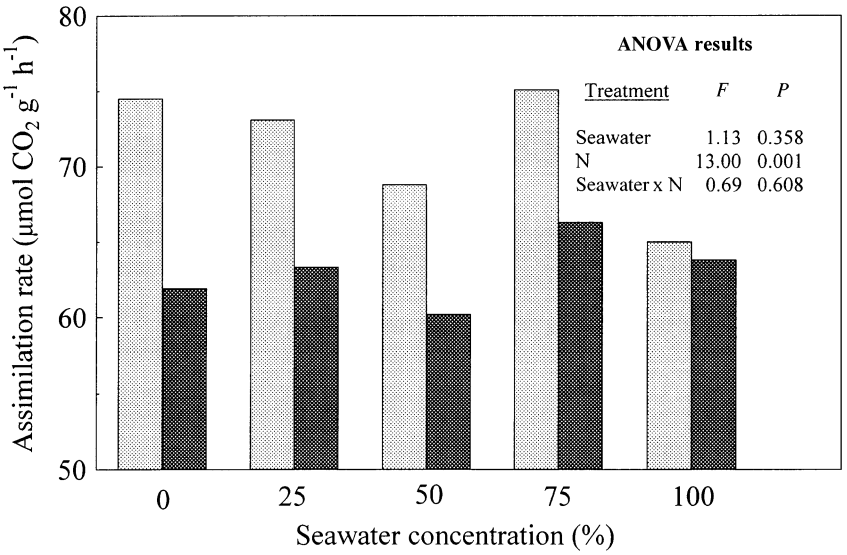

Fig. 6 Net CO_2 assimilation rate after 19 d exposure to different seawater concentrations, with (+N; grey bars) and without (–N; dark grey bars) inorganic N in *Turgidiusculum complicatulum*. All +N vs. –N differences significant at $P \leq 0.05$, except for the 100% seawater treatment. (ANOVA, analysis of variance).

Discussion

Thallus moisture content optima for photosynthesis reported here (225–350%) are similar to those (250–350%) found for *T. complicatulum* on Galindez Island on the Antarctic Peninsula (Huiskes *et al.*, 1997a). At optimum thallus moisture content, near-saturating light and favourable temperature (10 or 15°C), the average net assimilation rate of *T. complicatulum* (Fig. 1) was 70–90 μmol CO_2 g^{-1} h^{-1} (= 3.1–4.0 mg CO_2 g^{-1} h^{-1}), similar to maximum values (3–4 mg CO_2 g^{-1} h^{-1}) found for a *Peltigera* species on Marion Island (Smith, 1988) but higher than maximum values (0.11–0.8 mg CO_2 g^{-1} h^{-1}) reported for Antarctic lichens in general (Kappen, 1988; Longton, 1988). Of some 40 European and Arctic lichen species listed by Kallio & Kärenlampi (1975) and Longton (1988), only five showed maximum assimilation rates equalling those found here for *T. complicatulum*; most species showed rates about one order of magnitude lower.

The observation that salinity up to the level of undiluted seawater had no effect on the gas exchange or chlorophyll fluorescence characteristics of *T. complicatulum* agrees with the finding of Jacob *et al.* (1991) that photosynthesis in *P. crispa* is unaffected by salinity up to the level represented by 'standard' seawater (35‰), and suggests that the lichen is salt-tolerant, but not an obligate halophyte. However, thalli subjected to seawater inundation or salt spray in the field will experience increasing salt concentrations as they start drying out; a seawater-saturated lichen at 1000% moisture content will experience 4–5-times the osmotic stress of standard seawater by the time it dries out to the moisture content optimum for CO_2 assimilation. Jacob *et al.* (1991) showed that increasing salinity to levels above standard seawater causes a reduction in growth, photosynthesis and dark respiration of *P. crispa*. Hence, the combination of lichen desiccation and exposure to seawater might well limit the lichen's photosynthetic capacity in the field. The situation is probably much more complex than it might seem, since Huiskes *et al.* (1997b) showed that desiccation rate of *T. complicatulum* depends on the salinity of the habitat from which they occur (presumably via its effect on thallus salt content) and Huiskes & Moerdijk-Poortvliet (2000) have related this to differences in photosynthetic performance between thalli from saline and nonsaline habitats.

The model used here to fit the A : PPFD response curves is one of the earliest proposed (Smith, 1936) but provided very good fits to the data, even though we added the assumption that respiration rate in the light is equal to that in the dark at the same temperature. Other, more sophisticated (and more fashionable) models were tested, for example the nonrectangular hyperbola 'convexity' equation (Thornley & Johnson, 1990) and its derivative that takes respiration into account (Prioul & Chartier, 1977), but they did not increase the reliability of the net assimilation rate predictions. The data set used with the model did not include assimilation values at light levels above saturation (approx. 250–300 μmol m^{-2} s^{-1} PPFD), since we aimed to avoid photoinhibiting the thalli. However, the rapid increase in nonphotochemical quenching with increasing irradiance, and the subsequent attainment of high q_N values, at light levels that are not limiting for photosynthesis, suggests that the thalli can efficiently dissipate excess excitation energy to prevent photoinhibitory damage. The fact that even at light levels above saturation for electron transport a substantial fraction (approx. 20%) of PSII centres are still in the oxidized (open) state attests to the efficiency of this process. The increase in q_N under high light was associated with a very marked decrease in quantum yield (F_v/F_m; data not shown) which, however, increased again within an hour of the lichen being returned to low light values or to the dark. In fact, F_v/F_m recovered completely within 12 h in the

dark. This, plus the fact that the decrease in F_v/F_m in the light was due to a greatly depressed F_m and not to a change in F_o, suggests that the mechanism that decreases quantum yield in the light is a truly photoprotective, rather than photoinhibitory. Xanthophyll cycling is suggested as this mechanism, since Demmig-Adams *et al.* (1990) demonstrated that lichens with green algal phycobionts can form zeaxanthin rapidly under high irradiance. This response is coupled with a high capacity for nonradiative dissipation of excess excitation energy and an ability to maintain a sizeable population of open PSII centers, even under high light levels.

Both the modelled responses and the actual measurements showed that net carbon exchange in the lichen is overwhelmingly influenced by a strong elevation in respiration rate with increasing temperature. It is not known to what extent the mycobiont is responsible for this. Respiration in lichens is generally thought to be mycobiont-dominated but there are exceptions (Coxson *et al.*, 1982). Respiration in the free-living phycobiont, *P. crispa*, on Signy Island (maritime Antarctic) is strongly temperature-dependent, with Q_{10} values of 2–3 for temperatures between 5 and 20°C (Davey, 1989). Respiration rate of the alga at 20°C on Signy Island (0.5 mg C g^{-1} h^{-1}; Davey, 1989) is close to the average rate reported here for the lichenized form at 20°C (0.54 mg C g^{-1} h^{-1}; = 45 μmol CO_2 g^{-1} h^{-1}, Fig. 2). However, at 5°C, respiration rate of the alga (approx. 0.15 mg C g^{-1} h^{-1}) was greater than that of the lichen (0.06 mg C g^{-1} h^{-1}). Hence, increasing temperature from 5 to 20°C enhanced respiration rate nine-fold in the lichen (Q_{10} = 4.3), but only 2.5-fold (Q_{10} = 2.2) in the alga. This suggests that respiration of the mycobiont is an important component of the net C flux in the lichenized form, especially at higher temperatures. If the rate of respiration in the light is the same as that in the dark, then at 20°C and saturating PPFD, 'dark' respiration accounts for 35% of the carbon flux in *T. complicatulum* but only 13% in *P. crispa*.

Marion Island experiences a cool hyperoceanic climate without extremes of temperature and with high values of atmospheric moisture. Annual mean air temperature is 5.5°C with only a 1.4°C difference between the means of the warmest and coldest months. Annual precipitation is 2400 mm and no month receives less than 170 mm. Relative humidity rarely falls below 80%. No microclimatic measurements have been made in *Turgidiusculum* stands but light and temperature measurements taken every minute for 1 yr in a nearby moss layer (Blake, 1997) are summarized in Table 1. On average over the year, PPFD at the moss surface was above 50 μmol m^{-2} s^{-1} for 77% of daytime and temperature of the top 1 cm layer never exceeded 16.3°C; for 86% of daytime it was between 2 and 16°C. If this light : temperature regime applies to the *Turgidiusculum* mats, then under field conditions the CO_2 assimilation rate of hydrated thalli will be little affected by the large temperature dependence of respiration. The PPFD and temperature regime is such that hydrated thalli would exhibit maximal, or almost maximal, net photosynthesis rates for approx. 75% of the photoperiod over the year (stippled area on the response surface in Fig. 4). Even during the rest of the photoperiod when PPFD is lower, or at night (Table 1), temperatures do not rise to levels which would cause the rapid respiration rates found during the assimilation experiments. Hence, for most days the lichen, if sufficiently hydrated, would be expected to have a substantial positive net carbon balance.

Table 1 Microclimate at the surface of a moss cover close to where the *Turgidiusculum complicatulum* samples were collected. Daytime refers to the period from sunrise to sunset and night-time from sunset to sunrise. Measurements were made every minute for 1 yr

Daytime temperature	
Annual mean	6.1°C
Mean for warmest month	10.3°C
Mean for coldest month	2.2°C
Night-time temperature	
Annual mean	4.7°C
Mean for warmest month	9.9°C
Mean for coldest month	2.3°C
Annual mean daily minimum temp.	4.0°C
Absolute minimum temp.	0.1°C
Annual mean daily maximum temp.	6.9°C
Absolute maximum temp.	16.3°C
PPFD	
Annual mean (daytime only)	299 μmol m^{-2} s^{-1}
Maximum	1719 μmol m^{-2} s^{-1}
Annual mean within $^1/_4$ h of solar noon	465 μmol m^{-2} s^{-1}
Incidence of daytime PPFD values being > 50 μmol m^{-2} s^{-1}	77%
Incidence of daytime PPFD values being > 100 μmol m^{-2} s^{-1}	64%

In conclusion, the ecophysiological observations presented here accord with the finding of Gremmen *et al.* (1995) that standing crop of *T. complicatulum* on Petermann Island (Antarctic Peninsula) is strongly and positively related to substrate ammonium and phosphate concentrations but independent of substrate chloride levels. The high photosynthetic rate and the fact that inorganic N stimulated metabolic activity of the lichen (even though it depressed net photosynthesis rate), is consistent with the view that *T. complicatulum* is a nitrophilous lichen with the high production capacity characteristic of species from nutrient-rich habitats. The lichen has a photosynthetic response to light and temperature that enables it to maintain high rates of CO_2 assimilation under the microclimatic regime it experiences on Marion Island, provided the thallus can remain hydrated.

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