Thallus Moisture and Microclimatic Control of CO_2 Exchange of *Peltigera aphthosa* (L.) Willd. on Disko Island (West Greenland)

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Abstract

Carbon dioxide exchange of the foliose lichen *Peltigera aphthosa* and the microclimate of its habitat were measured in the field on Disko Island, West Greenland, during an 11-day-period in August 1987. The diurnal courses of net photosynthesis under natural and artificial water conditions were measured by means of a CO_2/H_2O-porometer. Thallus water content was the major limiting factor for the CO_2 exchange. In its natural habitat, *P. aphthosa* hardly ever reached the optimum water content (180–320% dry weight) for net photosynthesis during the measuring period. In the field, temperature of the moist (i.e. physiologically active) *Peltigera* thalli often exceeded 30°C. Laboratory measurements revealed that the optimum temperature of light saturated net photosynthesis was about 25°C. Photosynthesis of the lichen was unaffected subsequent to 30 min exposure of the thalli to temperatures just below 38°C but ceased if the temperature was above 47°C.

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1. Introduction

In Polar regions, lichens form a dominant element of the ecosystem. These cryptogams are well adapted to low temperatures, with standing −196°C (Kappen, 1973), and being able to recover rapidly from chilling to −30°C (Kallio and Heinonen, 1971). It has been demonstrated that Antarctic lichens show photosynthetic CO_2 fixation at temperatures below 0°C (Lange and Kappen, 1972; Kappen, 1989). In contrast, lichens in the hydrated state are heat sensitive organisms. The highest tolerance limit of 46.5°C was measured in a European *Cladonia* species (Lange, 1953) whereas *Peltigera scabrosa* from low arctic woodlands was already severely stressed at 25°C (MacFarlane and Kershaw, 1980).

In summer, solar radiation can raise the temperature of plants above ambient air temperature, even under an overcast sky (Körner and Larcher, 1988). In the subarctic tundra, sun radiation can elevate thallus temperature of the dark pigmented *Bryocaulon divergens* almost 40 K above air temperature (Gauslaa, 1984). During the night, thallus temperature gets lower than air temperature and may reach the freezing point as an effect of heat loss. The diurnal amplitude of thallus temperatures may consequently reach 50 K under clear sky conditions. Such diurnal temperature oscillations are not deleterious if the thallus is dry, but if it is moist, i.e. in the physiologically active state, the lichen requires adjustment of the physiological processes. On Disko Island, hot summer periods occur regularly and in this treeless region temperatures rise to values above 30°C on the ground. Cryptogams, as poikilohydrous organisms, normally desiccate quickly during a hot summer day and are highly resistant in the inactive state. Some lichens, however, such as *Peltigera aphthosa* which typically grows on moss or between grass and herbs on moist ground, may stay moist and active even during a hot summer day. It implicates that this lichen is at least temporally subjected to heat stress.

The aim of this study is to investigate in the field, to what extent *Peltigera aphthosa* is moist and photosynthetically active during a dry summer day and in which temperature range this is possible. By complementary experiments in the laboratory the heat tolerance of *P. aphthosa* was tested. Field measurements were carried out near "Arktisk Station" at Qeqertarssuaq (Godhavn), Disko Island, West Greenland, in August 1987. Laboratory experiments were conducted at Kiel, FRG. Until recently, field studies on net photosynthesis in arctic lichens with respect to habitat parameters have been carried out by Kershaw and Field, 1975; Larson and Kershaw, 1975; Carstairs and Oechel, 1978; Lechowicz, 1981; Moser et al., 1983. By means of the porometric method

(Lange et al., 1984) we were able to show in this study more closely the relations between thallus water content and photosynthetic performance of a lichen.

2. Materials and Methods

The species

The foliose lichen *Peltigera aphthosa* (L.) Willd. has a circumpolar distribution in arctic, boreal, and temperate regions where it grows on moss, soil, and plant debris in moist sites (Thomson, 1984). Its heteromerous thallus lacks a lower cortex as well as distinct rhizinae. The photobiont belongs to *Coccomyxa* (Chlorophyceae). Cephalodia containing *Nostoc* (Cyanobacteria) are present on the upper surface of the thallus. Aspects of the physiology particularly the nitrogen fixation, of *P. aphthosa* were discussed by Englund (1977).

Study sites

All field investigations were carried out near "Arktisk Station" at Qeqertarssuaq (69°15′N, 53°32′W; for details of topography and climate see Biebl, 1968). The microclimate of the habitat of *P. aphthosa* was recorded 1 km north-west of "Arktisk Station" at the bottom of the Lyngmarksfjeld massif at 56 m above sea-level. The vegetation in this area was an about 1 meter high *Salix glauca* formation, with *S. herbacea*, *Poa pratensis*, *Equisetum arvense*, *Luzula parviflora* and bryophytes in the understory.

Field measurements

Thallus temperature was recorded by small thermistor probes in two thalli of *P. aphthosa* each at a different aspect, one in a more sheltered site and the other openly exposed to SW. Air temperature was measured 1.5 m above the ground by a thermistor probe shielded against sun radiation. A GaAsP photodiode (calibrated against a Li-Cor LI-190 S quantum flux sensor) was used as a sensor of photosynthetic active radiation (PAR). Air humidity was recorded at a level of 2 cm above the SW-exposed thallus by a capacity probe (Humicap, Vaisala, Helsinki, SF). Data were collected every 5 min by a datalogger (Squirrel, Grant, Cambridge, UK). After a period of two weeks data were transferred to a Bondwell BW8 portable computer and stored on disk. Photosynthesis of *P. aphthosa* was measured at a site north of the building of "Arktisk Station". We used a CO_2/H_2O-Porometer (H. Walz, FRG) as described by Schulze et al. (1982) and Lange et al. (1984). The operation with

the porometer cuvette was carried out at a distance of 2 m from a tent in which the control and recording units were installed (Fig. 1).

Figure 1. CO_2/H_2O porometer head and igloo tent with the control device north of the building of "Arktisk Station".

Gas exchange was monitored in an open system by a differential IRGA (BINOS, Leybold Heraeus, Hanau, FRG) consisting of a H_2O-unit (0–5000 ppm H_2O) and a CO_2-unit ($-25\ldots+25$ ppm CO_2). The gas stream was dried by a cooling trap MGK-4 (H. Walz, FRG) before it entered the CO_2-unit. Data were collected by an external datalogger (DES, H. Walz, FRG), transferred to a Bondwell BW8 portable computer and stored on disk. Data were evaluated at Kiel by a Siemens PC-D2 computer using a calculation and plot program PHOTOPLOT especially designed by Schroeter and Heitland (unpublished).

The photosynthetic activity of the fresh thalli was measured every 2 hr. Three parallel samples of lobes (5–20 cm² in size) of larger *P. aphthosa* thalli were collected from their habitat near the microclimate measuring site. Water-loss during transportation was avoided by carrying the thalli in aluminium bags to the photosynthesis measuring site. In the following experiments, three *P. aphthosa* lobes in parallel were saturated in spring-water and blotted with filter paper (cf. Lange et al., 1984) in order to remove adhering water prior to the photosynthesis measurement. The photosynthetic rate of one lobe was

measured by a series of five or six runs, each integrating over a period of 1 min. Only the last two or three steady state values were taken as valid. Thallus water content was determined gravimetrically before and after each photosynthesis measurement. Net photosynthetic rates were referred to surface area and oven dry weight (24 hr, 105°C). The zero level of the IRGA was checked every hour and the measurements were corrected accordingly.

Laboratory measurements

Air-dry lichen thalli were transported to Kiel and cultivated in an illuminated and temperature-controlled chamber (quantum flux density 200 μmol $m^{-2}s^{-1}$ PAR, 12:12 hr photoperiod, 10°C, periodical moistening). The CO_2 exchange measurements were carried out with samples at around optimal moisture content (i.e. the moisture content at which rates of net photosynthesis were highest) by means of an open flow IRGA system (cf. Sancho and Kappen, 1989). Optimum temperature and upper and lower compensation points of net photosynthesis were determined at different irradiance levels. Two replicates were used at −5, 0, 5, 10°C and another two at 15, 20, 25, 30°C in order to avoid acclimation and stress effects.

Heat tolerance was determined according to Kappen and Smith (1980). Two replicates were used for each temperature treatment. The CO_2 exchange as an indicator of viability of the lichens was measured at 15°C and 400 μmol $m^{-2}s^{-1}$PAR before the heat treatment, as well as 7 and 20 days after the treatment. Vitality was indicated 20 days subsequent to the heat treatment by the degree of depression of CO_2 exchange rate as a percentage of the optimum rate prior to the treatment. Measurements of untreated parallel samples confirmed that a 20-day-cultivation in moist chambers under controlled conditions as described earlier did not affect the photosynthetic activity of the lichens.

3. Results

The temperature regime of *Peltigera aphthosa in situ* during the period between 8 and 18 August, 1987 is shown in Fig. 2. The daily maximum, minimum and mean thallus temperature in two *P. aphthosa* individuals were compared. During this period, the daily mean of thallus temperature varied between 7.3°C and 13.6°C in the SW-exposed thallus, and between 6.5°and 10.6°C in the more sheltered thallus. During a clear sunny day (e.g. 13 August), the diurnal amplitude runs up to more than 31 K in the exposed thallus. The maximum temperature was 34.2°C in the afternoon. This lichen was heated to
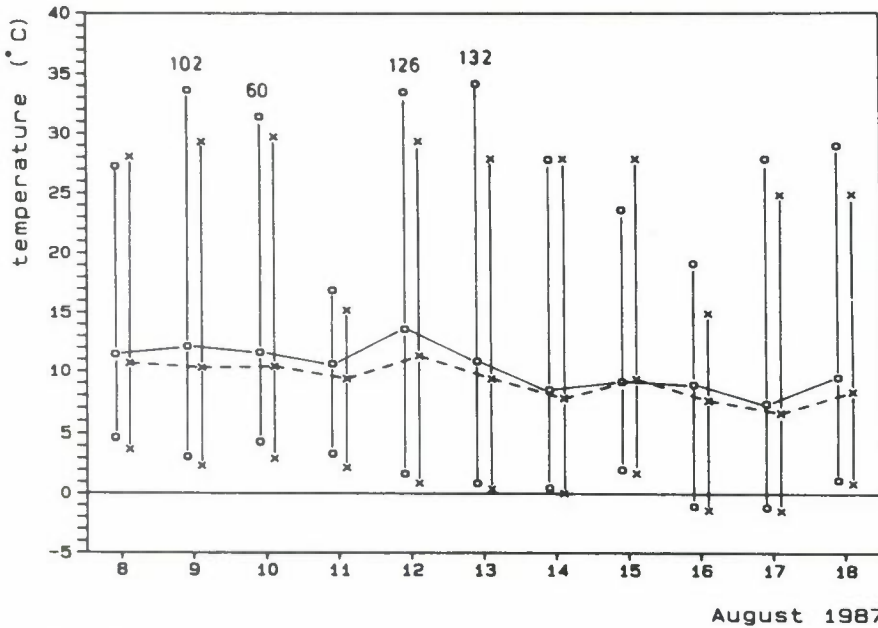
Figure 2. Daily maximum, minimum and mean thallus temperature (°C) in a sheltered (x, broken line) and a SW exposed (o, solid line) *P. aphthosa* thallus measured at the microclimatic study site near Qeqertarssuaq on August 8–18, 1987. Numbers indicate the time (min) of exposure to temperatures above 30°C.

temperatures above 30°C for a period of 132 min during this day. In contrast, thallus temperature went down to −1.5°C during the night of 16 to 17 August. In every case the thalli were soft and flexible; this indicates that *P. aphthosa* was moist in its habitat almost throughout the day.

Figure 3 shows the microclimatic habitat parameters during two subsequent days with contrasting climatic conditions in the SW-exposed *P. aphthosa* thallus. Under an overcast sky during 11 August, quantum flux density did not exceed 300 μmol m^{-2}s^{-1}PAR, and thallus temperature was 7 K above air temperature; the thallus temperature reached a maximum of 17°C around noon. Air humidity near the lichen always exceeded 90% during the day. On the following day which was clear and sunny, quantum flux density reached 1850 μmol m^{-2}s^{-1}PAR, and air humidity decreased to a minimum of 55% around noon. The thallus temperature reached 34°C, which was 18 K above that of ambient air. During the night, thallus temperature dropped under that of ambient air as a result of heat loss. The heat tolerance of *P. aphthosa* is shown in Fig. 4. An experimental 30-minute heat treatment at 38°C did not
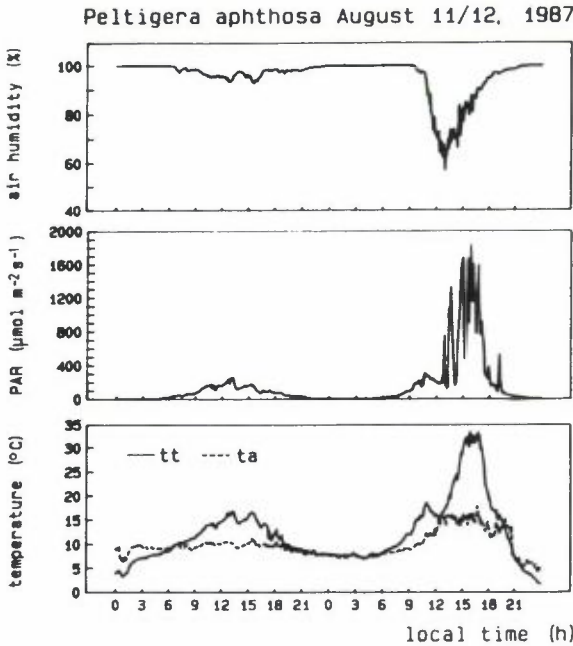
Figure 3. Relative air humidity (%), photosynthetic active radiation (PAR), and thallus temperature (°C), tt, solid line) at the surface of *P. aphthosa* and air temperature (°C, ta, broken line) at the microclimate study site near Qeqertarssuaq on August 11–12, 1987.

decrease the photosynthetic rate of *P. aphthosa*. However treatment at temperatures above 40°C caused the optimum net photosynthetic rate to decrease below 50% of that in the untreated state. Thalli subjected to more than 47°C were not able to regain positive net photosynthesis during a 20-day-recovering period.

The diurnal CO_2 exchange pattern of *P. aphthosa* in relation to thallus water content, irradiance and temperature in the field is illustrated in Fig. 5 (naturally moist thalli) and Fig. 6 (thalli sprayed with spring-water).

Under natural conditions the thallus water content of *P. aphthosa* ranged between 50 to 160% of dry weight, and apart form a slight depression around noon no tendency of water loss was apparent during 15 August. The increased water content of the specimens, collected the subsequent morning, indicated that the lichen yielded water during the night (Fig. 5). As a response, the photosynthetic rates were increased and reached higher values at a lower irradiance level than during the foregoing morning.
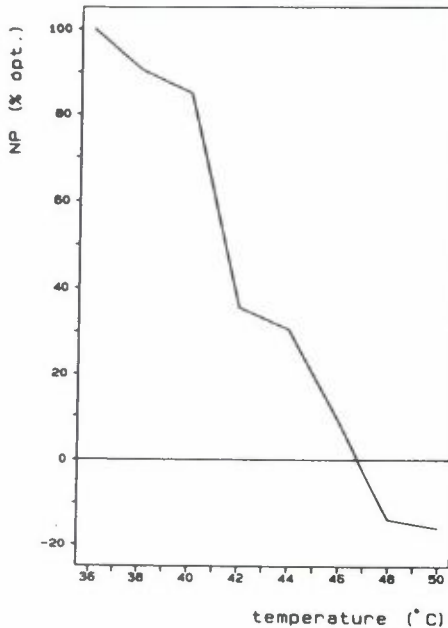
Figure 4. Heat tolerance limit for *P. aphthosa*, expressed as the percentage of CO_2 exchange value 20 days after the heat treatment related to the values prior to a 30 min heat treatment at the temperature (°C) given on the abscissa. Values are means of the rates of two replicates.

In the afternoon of August 16, artificially water-soaked samples of *P. aphthosa* were investigated (Fig. 6). Under an overcast sky, temperature and irradiance remained nearly constant from 13.40 hr to 17.40 hr. Consequently, changes of the photosynthetic rates were mainly caused by the thallus water content. In the highly soaked state a weak depression of net photosynthesis was apparent. Thereafter photosynthesis stayed on a high level within a wide range of water contents. When the water content underwent 100% d.wt., a limiting effect was visible in both tested specimens. Figure 7 illustrates how net photosynthesis depends on the thallus water content of two different samples. Irrespective of the individual variation of the dry matter contents, the response of the thallus lobes is exactly the same. Net photosynthesis starts at a water content of 60% d.wt. The photosynthetic rate is highest at a water content between 200 and 300% d.wt. A decrease is apparent as soon as the water content is higher than 320% d.wt.

The temperature dependency of net photosynthesis was investigated in the laboratory at 48 different temperature/irradiance combinations (Table 1).
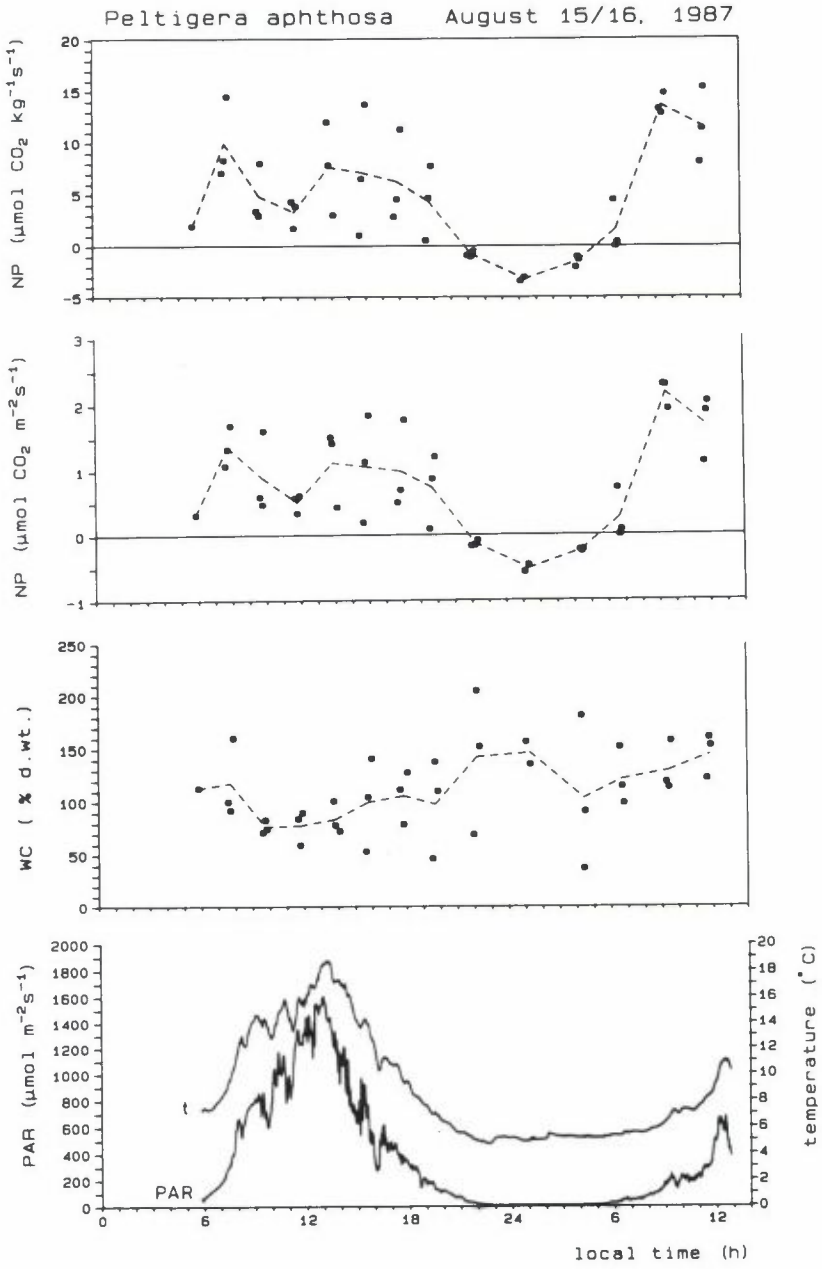
Figure 5. *In situ* net photosynthetic response in *P. aphthosa* related to dry weight (μmol CO_2 kg^{-1}s^{-1}) and surface area (μmol CO_2 m^{-2}s^{-1}), percent natural water content (by dry weight), photosynthetic active radiation (PAR) and thallus temperature (°C) on August 15–16, 1987. Broken lines indicate the means of subsequent measurements with two or mostly three specimens.
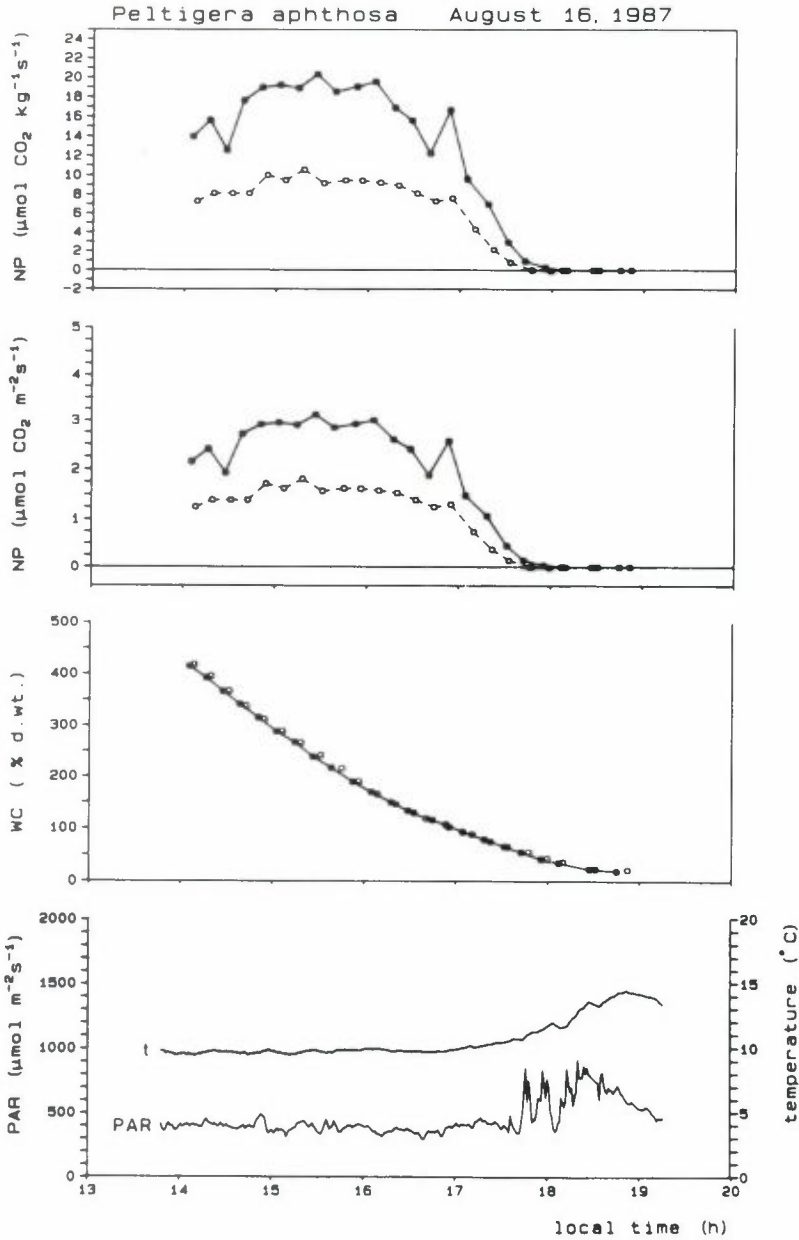
Figure 6. Time course of net photosynthesis (NP) related to dry weight (μmol CO_2 $kg^{-1}s^{-1}$) and surface area (μmol CO_2 $m^{-2}s^{-1}$) in two replicates of *P. aphthosa* (solid line = black circles, broken line = open circles) with water contents decreasing from an initial value of 400% dry weight (WC by dry weight). Natural irradiance (PAR) and temperature conditions (°C) under overcast sky on August 16, 1987.

Table 1. Lower and upper temperature compensation points (TCP) and optimum temperature of net photosynthesis determined at various irradiance levels (PAR). Results from laboratory measurements carried out within a temperature range from −5 to +30°C.

PAR (μmol m^{-2}s^{-1})	Lower TCP (°C)	Upper TCP (°C)	Opt. Temp. (°C)
700	±5	>30	25
450	±5	>30	20
240	±5	>30	12
120	±5	>30	10
60	±5	28	5

The lower temperature compensation points at all irradiance levels are below −5°C; the upper temperature compensation points are higher than 30°C at irradiances higher than 60 μmol m^{-2}s^{-1}PAR. The optimum temperature increases from 5°C at 60 μmol m^{-2}s^{-1}PAR to 25°C at light saturation level (700 μmol m^{-2}s^{-1}PAR).
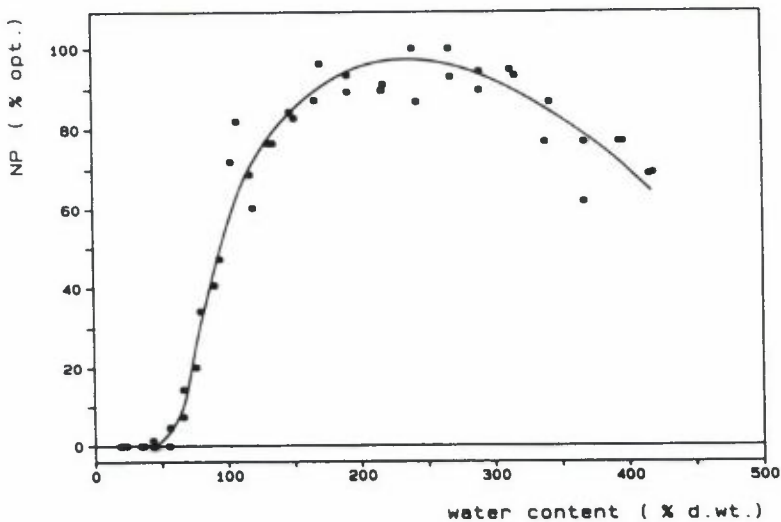

Figure 7. Net photosynthetic response (NP, related to dry weight as the percentage of maximum rate) of *P. aphthosa* to percent thallus water content (by dry weight) at 9.5 to 12°C and 330 to 460 μmol m^{-2}s^{-1} PAR. Curve fitted by eye.

4. Discussion

The data presented in this study demonstrate that thallus temperatures of *Peltigera aphthosa* can exceed 30°C for periods of more than 2 hr a day in Greenland during summer. It is well established (Lange, 1953; Kappen et al., 1980) that the poikilohydrous lichens usually dry out if temperatures are that high, and stay in an inactive, highly resistant state. The thalli of *P. aphthosa*, however, stayed moist throughout the day and gained a positive carbon balance during the period under consideration. Our measurements confirmed that *P. aphthosa* is photosynthetically productive at temperatures up to 38°C. This temperature was not reached during the period of our investigations, consequently the tolerance limit (40°C) was not reached. The remarkable adaptation of *P. aphthosa* to high temperatures was also emphasized by MacFarlane and Kershaw (1980) in a comparison with other *Peltigera* species in the low arctic. The capability of gaining positive net photosynthetic rates within a range of more than 35 K and of shifting the photosynthetic optimum temperature from 5°C at low light to 25°C at light saturation level (Table 1) indicates a high plasticity of *P. aphthosa*.

Morphology (Larson, 1979, 1981) and anatomy (Ried, 1960, Sancho and Kappen, 1989) are known to influence the water retention capacity of lichen thalli. *Peltigera aphthosa* consists of up to 1000 μm thick, curved lobes with ascending edges and a smooth upper surface. The surface-area/weight ratio, which is used for the estimation of evaporation rates (Larson and Kershaw, 1976), has a mean value of 62 cm^2g^{-1} in *P. aphthosa* according to our measurements (65 specimens tested; only upper surface considered). This value is remarkably low, compared to those determined by Larson and Kershaw (1976) in arctic and subarctic fruticose lichens (e.g. *Cetraria nivalis*: 370 cm^2g^{-1}, *Cladonia stellaris*: 625 cm^2g^{-1}).

Thallus shape and the low surface-area/weight ratio in *P. aphthosa* are probably important factors in preventing rapid water loss. Also the anatomy of *P. aphthosa* shows that this lichen is adapted to maintain a high thallus water content for extended periods of time. Like other *Peltigera* spp., *P. aphthosa* has a thick medullary layer of loosely interwoven hyphae but no lower cortex. The loose medullary tissue at the lower surface of *Peltigera* was termed "pilema" by Hannemann (1973). The same author observed that liquid water was quickly absorbed and retained (as capillary water) by the pilema of *P. canina*. Similar findings were earlier reported by Smyth (1934), Ried (1960), and others. Smith (1961) assumed that the medulla of *P. polydactyla* "may function as a primitive water reservoir for the metabolic more active" parts of the thallus. Moreover, Snelgar and Green (1981) stated that the medullary

tissue of *Pseudocyphellaria dissimilis* varied in thickness as a response to environmental conditions; thalli with a thicker medulla were found to show higher water storage capacity and lower desiccation rates.

In the present experiments *P. aphthosa* reached a water content of ca. 400% d.wt. if soaked in water and subsequently blotted. However, highest net photosynthetic rates were achieved at ca. 250%, and the thallus water compensation point was reached at ca. 50%. These results with *P. aphthosa* having a green algae photobiont are in agreement with the values found by Lange and Matthes (1981) in *P. canina* and by Hahn et al. (1989) in *P. rufescens*, two species with *Nostoc* as the main photobiont. It is concluded that in all the three *Peltigera* species, the moisture-related compensation point and optimum of photosynthesis are mainly determined by the anatomy of the mycobiont.

Peltigera aphthosa typically grows in slightly shaded places with high ground moisture, a "hygrophytic performance" according to Hansen (1978). On Disko Island, we found *P. aphthosa* in partial shelter of *Salix glauca* and growing on moss. Under these conditions the thalli stayed at a suboptimal thallus water content throughout the day, even during hot summer days, whilst other lichens, such as *Usnea sphacelata* and *Umbilicaria vellea* near the site of our CO_2 exchange measurements, were air-dry and inactive except for short periods after morning dew fall.

The photosynthetic gain of *P. aphthosa* under natural (= suboptimal) water conditions is in the same range as that of *P. rufescens* from a central European habitat (Hahn et al., 1989). Artificially soaked thalli of *P. aphthosa* had a maximum photosynthetic rate of 3.1 μmol CO_2 m^{-2}s^{-1} (20.4 μmol CO_2 kg^{-1}s^{-1}) at 9.8°C, 404 μmol m^{-2}s^{-1}PAR and optimum water content (240% d.wt.). The maximum net photosynthetic rate of about 1.5 μmol CO_2 m^{-2}s^{-1} (20–26°C, 900 μmol m^{-2}s^{-1}PAR) of *P. aphthosa* from Greenland reported by Eckardt et al. (1982) seems rather low, but information about water content and age of the thalli is lacking. Our material of *P. aphthosa* consisted of young, vigorously growing lobes. As marginal and central parts of *P. aphthosa* thalli generally show higher photosynthetic rates than the older, basal parts (Englund, 1977), the carbon balance of whole thalli will certainly be lower than in the present study.

Our data indicate a great individual variation in net photosynthetic rates related to dry weight or surface area in different samples. Therefore a general conclusion about the water content dependency of net photosynthesis is only possible by comparing relative values as shown in Fig. 7. Consequently, intraspecific variations of photosynthetic data that are related to dry weight or surface area only, as in several other lichen studies, should be interpreted carefully.

Acknowledgements

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