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Investigations on the CO_2 Exchange of Lichens in the Alpine Belt. II. Comparative Patterns of Net CO_2 Exchange in *Cetraria islandica* and *Flavocetraria nivalis*

By

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With 8 Figures

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Summary

REITER R. & TÜRK R. 2000. Investigations on the CO_2 exchange of lichens in the alpine belt. II. Comparative patterns of net CO_2 exchange in *Cetraria islandica* and *Flavocetraria nivalis*. – Phyton (Horn, Austria) 40 (1): 161–177, 8 figures. – English with German summary.

The CO_2 exchange of two fruticose alpine lichen species was compared with respect to their thallus water content, light, temperature and moisture in the field and in the laboratory. Maximum net photosynthesis in both lichens was similar in the field, but in the laboratory *Cetraria islandica* had higher net CO_2 uptake rates than *Flavocetraria nivalis*. The light compensation point of *Cetraria islandica* was lower than those of *Flavocetraria nivalis* and increased with increasing temperature. The upper temperature compensation point was higher in *Cetraria islandica* than in *Flavocetraria nivalis*. Both lichens had similar moisture compensation point in the field and in the laboratory. The maximal and minimal thallus water content was lower in *Cetraria islandica* in comparison with *Flavocetraria nivalis*.

In the field hydration is the most important factor which determines the pattern of CO_2 exchange. CO_2 exchange was detected during the daytime and no nocturnal respiration was recorded. Total period of NP was ca. 52 % and ca. 45 % of time the lichens were inactive. Less but still positive NP was found when the lichens were frozen respectively when air temperature was far below the freezing point.

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Zusammenfassung

REITER R. & TÜRK R. 2000. Untersuchungen über den CO_2-Gaswechsel von Flechten in der alpinen Stufe. II. Vergleichende Muster des CO_2-Gaswechsels von *Cetraria islandica* und *Flavocetraria nivalis*. – Phyton (Horn, Austria) 40 (1): 161–177, 8 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Der CO_2-Gaswechsel von zwei alpinen Strauchflechten wurde in Bezug auf Wassergehalt, Licht, Temperatur und Feuchte im Freiland und im Labor untersucht. *Cetraria islandica* und *Flavocetraria nivalis* wiesen im Freiland eine vergleichbare maximale Nettophotosynthese auf, aber im Labor hatte *Cetraria islandica* eine höhere CO_2-Aufnahmerate als *Flavocetraria nivalis*. Der Lichtkompensationspunkt von *Cetraria islandica* war niedriger als jener von *Flavocetraria nivalis* und stieg bei beiden Flechten mit der Temperatur an. Der obere Temperaturkompensationspunkt lag bei *Cetraria islandica* höher als bei *Flavocetraria nivalis*. Beide Flechten hatten einen ähnlichen Feuchtekompensationspunkt im Freiland als auch im Labor. Der maximale und minimale Wassergehalt des Thallus war bei *Cetraria islandica* niedriger als bei *Flavocetraria nivalis*.

Im Freiland war die Verfügbarkeit von Wasser der dominierende Faktor für das CO_2-Aufnahmemuster. Der CO_2-Gaswechsel wurde zwischen Sonnenaufgang und -untergang gemessen, die nächtliche Respiration wurde nicht berücksichtigt. Während der gesamten Periode nutzten die Flechten ca. 52 % der Zeit für Nettophotosynthese und waren ca. 45 % inaktiv. Bei gefrorenen Flechten, bzw. bei Lufttemperaturen weit unter dem Gefrierpunkt, wurde eine geringe, aber noch positive Nettophotosynthese aufgezeichnet.

Introduction

In a previous publication the response of net CO_2 exchange to environmental factors of two fruticose lichens *Cladonia mitis* and *Thamnolia vermicularis* and an umbilicate lichen *Umbilicaria cylindrica* was investigated (REITER & TÜRK 2000). The present study should provide additional datas by two further fruticose lichens, *Cetraria islandica* and *Flavocetraria nivalis*. These lichens were investigated together with the first one under the same microclimatical conditions in the field and in the laboratory.

Abbreviations: DW: dry weight, LCP: light compensation point, MCP: moisture compensation point, NP: net photosynthesis, PPFD: photosynthetic photon flux density, TCP: temperature compensation point, WC: water content.

Materials and Methods

Two frequent alpine fruticose terricolous macrolichens, *Cetraria islandica* (L.) ACH. and *Flavocetraria nivalis* (L.) KÄRNEFELT were chosen for the CO_2 exchange investigations.

For the field measurements the measuring station was situated close to the Hochalpine Forschungsstation des Hauses der Natur in the Nationalpark Hohe Tauern (Central Alps of Austria) in a height of 2300 m. The lichens were fixed in wire mesh baskets and exposed to the natural environment conditions. The CO_2 exchange in the field was detected by means of a compact CO_2/H_2O porometer (CQP-130, Walz, FRG).

The BINOS 100 infrared gas analyzer (Leybold Heraeus, Hanau, FRG) was used in the open flow system operating in the differential mode. Photosynthetic photon flux density was registered by means of a Quantum Sensor (LI-190 SZ, Lambda Instrument Corporation, USA) which was positioned close to the cuvette. Air temperature and relative humidity were detected by means of a datalogger (testo 454, FRG). Microclimate was recorded every 5 minutes and afterwards averaged to hourly means. A digital Baro-/Vacuum-Meter (GDH 12 AN, Greisinger electronic, FRG) was used to measure daily air pressure. The liquid precipitation was recorded by an Ombrometer. The actual WC was determined gravimatrically by an electronic digital balance (SBC-41 Scaltec Instruments, FRG).

In the laboratory, a compact minicuvette system (CMS-400, Walz, FRG) registered the CO_2 exchange under controlled microclimatic conditions. The source of radiation was a halogen lamp with fibre optics (FL-400, Walz, FRG). Prior to the experiments the lichen were submersed 10 minutes in de-ionised water in order to saturate the thalli. Adhering droplets were removed afterwards by shaking. The response of CO_2 exchange to altered microclimate was measured once in the laboratory.

CO_2 exchange data were related to oven dry weight (104 °C, 24 h). Graphs were created and curves were fitted using SigmaPlot 4.01.

More detail about the site description and the procedure of measuring is found in REITER & TÜRK 2000. Further information about CO_2 exchange measurements is given by LANGE & TENHUNEN 1984, LANGE & al. 1984, 1985, KAPPEN & al. 1990, LANGE & al. 1993.

Results

Field measurements

The field measurements were undertaken during the periods August 28th to September 10th and October 21st–25th 1997. In 19 days datas over 230 hours were gained. The recorded time started before dawn and finished after dusk. Thus no nocturnal respiration was recorded.

Precipitation

Water availability is the foremost factor which determine the pattern of CO_2 exchange. Precipitation was found in form of rain, snow, fog, dew fall and high relative humidity. More than the half of the recorded liquid precipitation (32.1 mm) was fallen on September 7th (14.3 mm). As typical for the alpine zone snowfall occurred also in summer. In the morning on August 29th (Fig. 1) the ground was covered by snow with a depht of 14 mm. Snow disappeard before midday on August 30th. In the past, the correlation between WC and CO_2 exchange was the basis for the establishment of different 'types' of CO_2 exchange (eg. HAHN & al. 1993, REITER & TÜRK 2000).

Under dry weather conditions as seen on September 1st, 2nd (Fig. 1, 2) and October 23rd (Fig. 4) relative air humidity droped down to 25–30 %

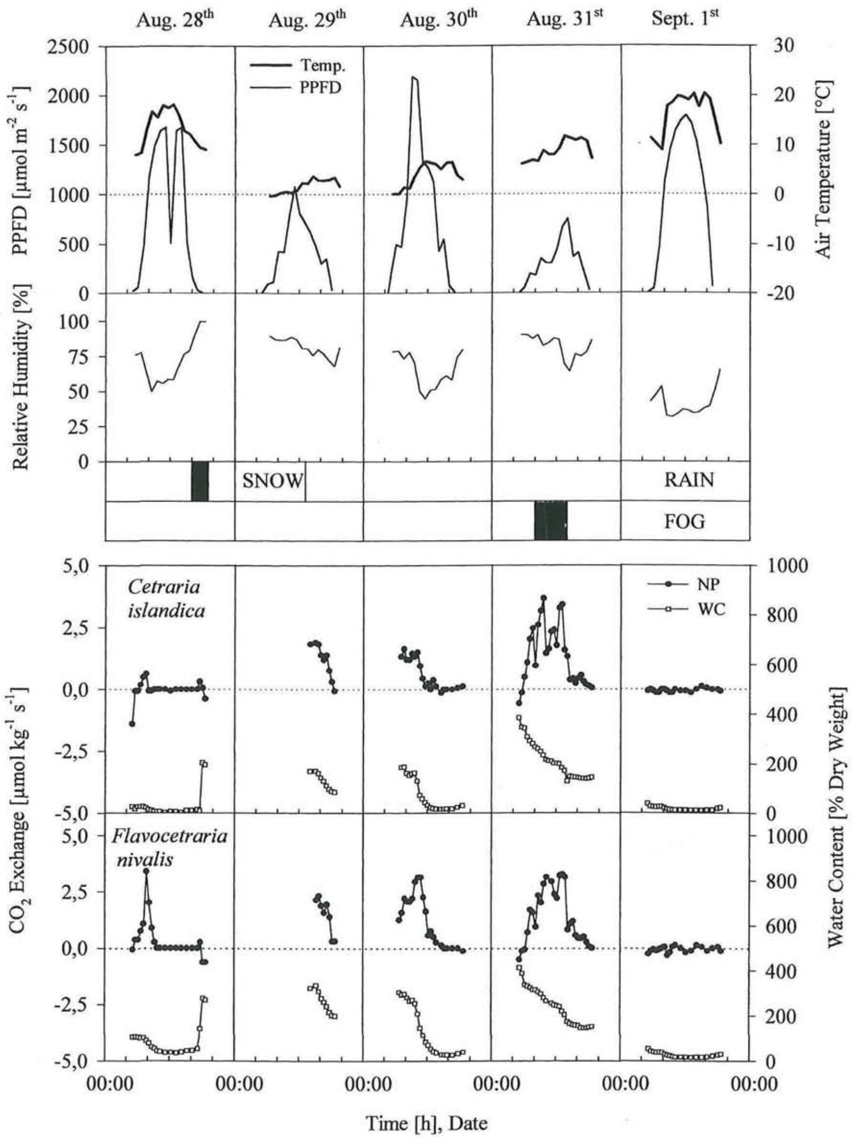
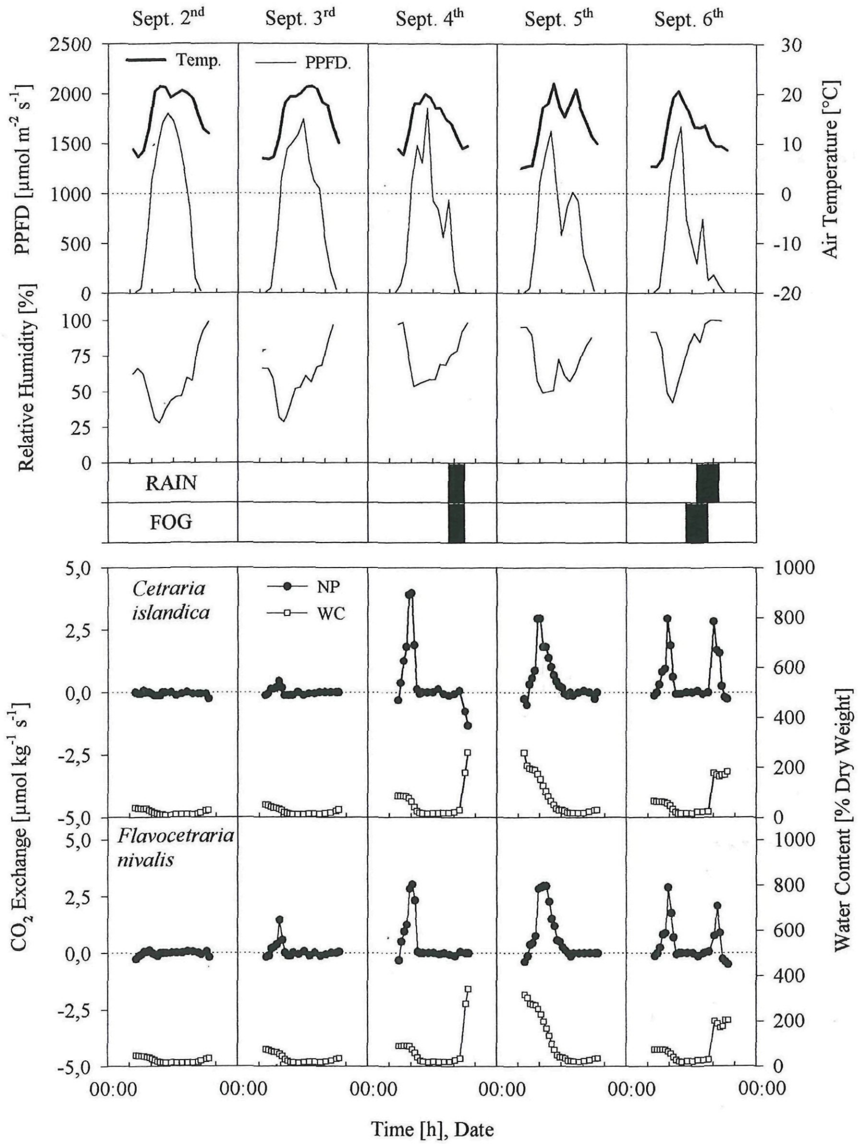
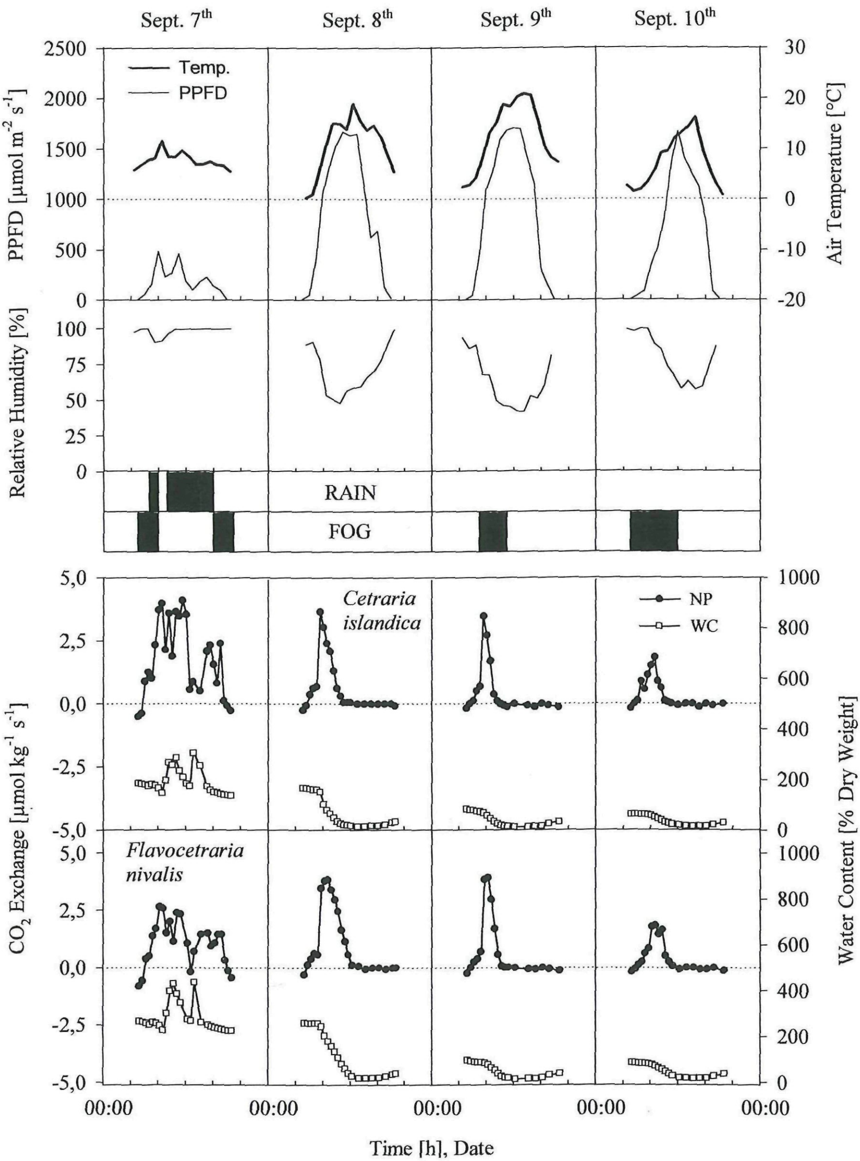
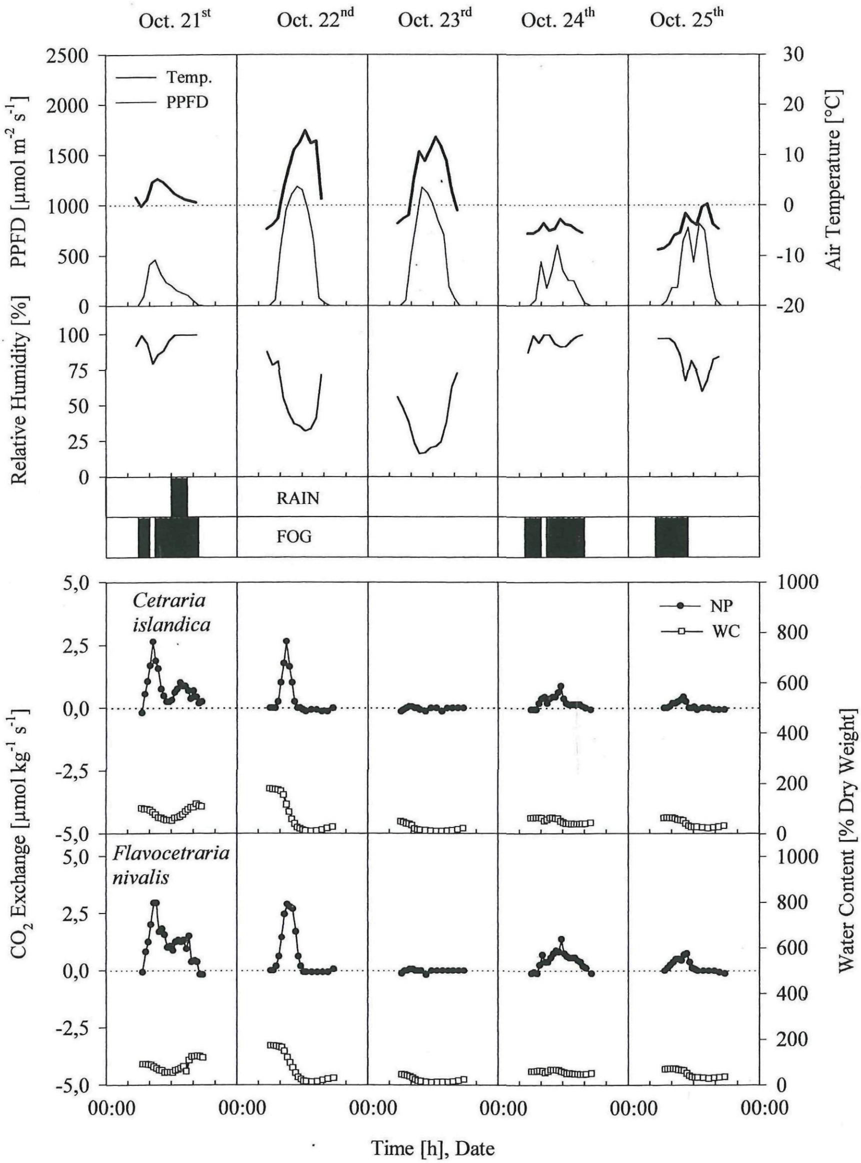


Fig. 1-4. Diurnal courses of CO_2 exchange (dots) and thallus water content (squares) for *Cetraria islandica* and *Flavocetraria nivalis*. Individual days are separated by vertical lines. The corresponding air temperature, incident photosynthetic photon flux density as well as the time period with rain and fog are shown in the upper diagram. Microclimatical datas were averaged to produce hourly means.



Sept. 2nd
Sept. 3rd
Sept. 4th
Sept. 5th
Sept. 6th
Temp.
PPFD.
PPFD [µmol m-2 s-1]
Air Temperature [°C]
2500
2000
1500
1000
500
0
30
20
10
0
-10
-20
Relative Humidity [%]
100
75
50
25
0
RAIN
FOG
Cetraria islandica
NP
WC
Flavocetraria nivalis
CO2 Exchange [µmol kg-1 s-1]
Water Content [% Dry Weight]
5,0
2,5
0,0
-2,5
-5,0
1000
800
600
400
200
0
00:00
Time [h], Date


Sept. 7th
Sept. 8th
Sept. 9th
Sept. 10th
Temp.
PPFD
PPFD [µmol m-2 s-1]
Air Temperature [°C]
Relative Humidity [%]
RAIN
FOG
Cetraria islandica
Flavocetraria nivalis
NP
WC
CO2 Exchange [µmol kg-1 s-1]
Water Content [% Dry Weight]
00:00
Time [h], Date


Oct. 21st
Oct. 22nd
Oct. 23rd
Oct. 24th
Oct. 25th
Temp.
PPFD
PPFD [µmol m-2 s-1]
Air Temperature [°C]
Relative Humidity [%]
RAIN
FOG
Cetraria islandica
Flavocetraria nivalis
NP
WC
CO2 Exchange [µmol kg-1 s-1]
Water Content [% Dry Weight]
Time [h], Date

already in the morning and caused low thallus WC down to 12 %. Consequently no CO_2 exchange was detected during the whole day.

In more than the half of all recorded diurnal courses (August 28th, 30th; September 3rd, 4th, 5th, 8th, 9th, 10th; October 22nd, 25th) the thalli were hydrated during the night but in the daytime no further water sources were available. Thus just in the morning NP was possible. With increasing temperature the WC decreased gradually and CO_2 exchange ceased after a short period of respiration. The length of NP and its maximum is dependent on the level of WC. In average 2.5–7 hours were used for NP with maximal rates between 0.4–4.0 µmol CO_2 kg^{-1} s^{-1}. On some days rainfall occurred in the afternoon and the lichens were hydrated again. With sufficient radiation a second peak of NP could be registered (August 28th, September 6th) but when actual PPFD was lower than the LCP respiration was measured (September 4th).

Continuously hydration of the lichens enabled CO_2 exchange during the whole daytime (August 29th, 31st, September 7th, October 21st, 24th). Changing WC depended on changing precipitation and the actual NP rate is influenced by illumination. Fog is able to delay the drying of the thalli as seen on August 31th and October 25th. When fog disappeared WC decreased and the NP curve declined rapidly till the lichens became inactive.

On October 24th (Fig. 4) no rain was detected but almost continuous fog was the cause for the high relative humidity with values around 100 % before midday. The WC was in equilibrium with the water vapor of the air. The whole day air temperatures remained below the freezing point and this was a pronounced shelter against waterlosses. The maximal rate of CO_2 uptake was measured when radiation increased for a short time up to 1470 µmol m^{-2} s^{-1} in the height of 0.9 (*Cetraria islandica*) and 1.4 µmol CO_2 kg^{-1} s^{-1} (*Flavocetraria nivalis*).

Light

With sufficient WC the curve of CO_2 exchange is strongly determined on the present amount of radiation. On cloudless days the maximal PPFD is dependent upon the season. On September 1st (Fig. 1) the level of radiation was 1800 µmol m^{-2} s^{-1}, but on October 22nd (Fig. 4) due to the lower sun angle only 1200 µmol m^{-2} s^{-1} was reached at midday. On August 30th (Fig. 1) snow cover caused high reflexion so that radiation rates over 2000 µmol m^{-2} s^{-1} were registered. The maximum on this day was 2700 µmol m^{-2} s^{-1}. In spite of high radiation the maximal NP was not reached on this day. Clouds and fog are able to reduce strongly the incident light. As seen on September 7th (Fig. 3) around midday the cloudiness became heavily and the PPFD was reduced. Thus the NP of *Flavocetraria nivalis* became negative with –0.2 µmol CO_2 kg^{-1} s^{-1} and 270 % WC at 50 µmol m^{-2} s^{-1}

PPFD. In contrast NP of *Cetraria islandica* did not fall below the LCP and reached 0.6 μmol CO_2 kg^{-1} s^{-1} with 175 % WC at 60 μmol m^{-2} s^{-1} PPFD.

Temperature

At the alpine sites the heat input can be very different. In summer air temperature can fall below to the freezing point and remain under 5 °C throughout the day (August 29th). On the other hand on clear days 25 °C and higher were reached (September 2nd, 5th, 9th). In autumn, in the morning frequently frost occurred and the lichens were frozen till 30 minutes after direct sunshine reached the measuring station (October 22nd–25th). Under these circumstances less but still positive CO_2 uptake could be detected. For instance on October 22nd frozen lichens reached a NP rate of 1.0 (*Cetraria islandica*) and 1.5 μmol CO_2 kg^{-1} s^{-1} (*Flavocetraria nivalis*) at sunrise with air temperatures of 2.5–3.5 °C and 535 μmol m^{-2} s^{-1} PPFD. Even with air temperature of –8 °C NP (0.13 μmol CO_2 kg^{-1} s^{-1}) was detected in *Flavocetraria nivalis* on October 25th (Fig. 4).

Laboratory measurements

Light

All experiments in the laboratory with altered light conditions were made with a constant temperature of 15 °C. The LCP of *Cetraria islandica* at optimal WC was 76 μmol m^{-2} s^{-1} PPFD. In the field lowest LCP was detected with much lower values of 11 μmol m^{-2} s^{-1} PPFD at 1.5-2 °C. *Flavocetraria nivalis* showed with optimal saturated thallus a similar LCP of 79 μmol m^{-2} s^{-1} PPFD. In the field with temperatures of 3-4.5 °C a LCP of 17 μmol m^{-2} s^{-1} PPFD could be detected (Table 1). Light saturation of CO_2 uptake was not reached with a PPFD of 2000 μmol m^{-2} s^{-1} and optimal WC (Fig. 5).

Temperature

Cetraria islandica has similar maximal NP rates at 30 and 2 °C with 2.0 respectively 1.8 μmol CO_2 kg^{-1} s^{-1}. The highest CO_2 uptake was detected at 20 °C with 4.6 μmol CO_2 kg^{-1} s^{-1}. At 10 °C a maximal rate of 3.3 μmol CO_2 kg^{-1} s^{-1} was observed. Maximal respiration was reached at 30 °C with -6.6 μmol CO_2 kg^{-1} s^{-1} (Fig. 7). *Flavocetraria nivalis* reached no positive NP at 30 °C and 1000 μmol m^{-2} s^{-1} PPFD at all WC values. At 20 °C maximal NP was detected with 4.6 and at 10 °C a rate of 4.0 μmol CO_2 kg^{-1} s^{-1} was registered. At 2 °C with 2.5 μmol CO_2 kg^{-1} s^{-1} more than the half of maximal NP was reached. Highest respiration (-11.0 μmol CO_2 kg^{-1} s^{-1}) was registered at 30 °C (Fig. 7).

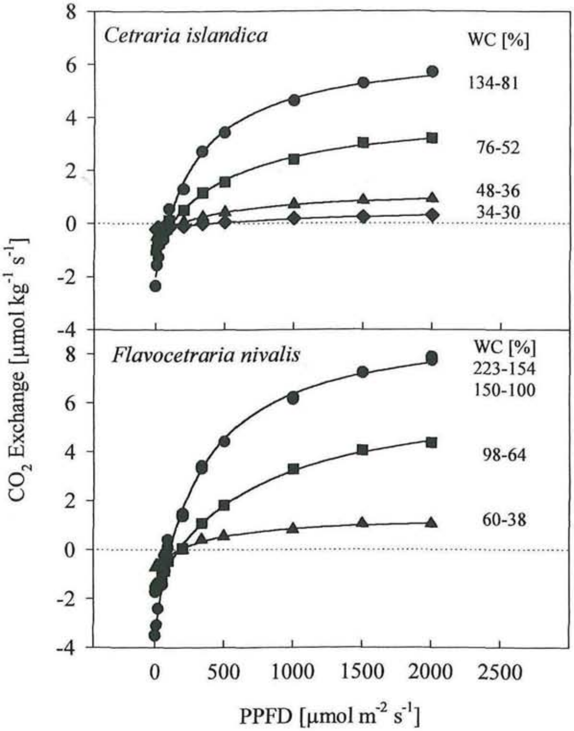


Fig. 5. Response of CO_2 exchange to photosynthetic photon flux density (PPFD) for *Cetraria islandica* and *Flavocetraria nivalis* at different water contents (WC) and 15 °C in the laboratory.

Thallus water content

In order to reach maximum WC, the lichens were submersed 10 minutes long in de-ionised water; *Cetraria islandica* reached a maximal hydration of 150 % and *Flavocetraria nivalis* of 240 %. In the field the lichens were higher saturated with water than in the laboratory. Their maximal WC was recorded on September 7th (Fig. 3), a day with long lasting precipitation. Under this conditions *Cetraria islandica* hat a maximal WC of 310 % and *Flavocetraria nivalis* of 440 %. Optimal WC in the laboratory of 100 % was found in *Cetraria islandica* and of 100–150 % in *Flavocetraria nivalis*. Minimal WC was detected in the field with 8 % WC (*Cetraria islandica*) and 12 % (*Flavocetraria nivalis*).

The moisture compensation point (MCP) was determined from field measurements from 5 diurnal courses (September 4th, 5th, 8th, 9th and October 22nd). *Cetraria islandica* had the lowest MCP of 18 % and *Flavocetraria nivalis* is characterised with 23 %. In the laboratory MCP became lower with increasing temperature respectively illumination. Lowest MCP was found at 30 °C and 1000 µmol m^{-2} s^{-1} PPFD of *Cetraria islandica* with 20 % and of *Flavocetraria nivalis* of 17 % (Table 1).

Maximal CO_2 exchange

In the laboratory maximal CO_2 uptake was reached at 2000 µmol m^{-2} s^{-1} PPFD and 15 °C. *Cetraria islandica* had a maximal NP at 5.6 µmol CO_2 kg^{-1} s^{-1}. A higher rate was attained by *Flavocetraria nivalis* at 8.0 µmol CO_2 kg^{-1} s^{-1}. In the field lower maximal CO_2 uptake was similar in both lichens with approximately 4.0 µmol CO_2 kg^{-1} s^{-1} (Table 1).

Table 1.
Comparison of CO_2 exchange results in the field and in the laboratory.

	Cetraria islandica		*Flavocetraria nivalis*	
	Field	Laboratory	Field	Laboratory
Maximum CO_2 uptake [µmol kg^{-1} s^{-1}]	4.1	5.6	3.9	8.0
Maximum CO_2 release [µmol kg^{-1} s^{-1}]	–	–6.6	–	–11.0
Light Compensation Point [µmol m^{-2} s^{-1}]	11	76	17	79
Moisture Compensation Point [% DW]	18	20	23	17
Maximal Water Content [% DW]	307	150	437	241
Minimal Water Content [% DW]	8	–	12	–

Discussion

The active period of the lichens is obviously strongly determined by the WC. The water uptake capacity is mainly determined by morphological and anatomical features. As illustrated in Fig. 8, *Cetraria islandica* was active in 46 % of the observed time (14 hours) and 54 % of it inactive. 41 % of active time were used for NP, 5 % for respiration, respectively. *Flavocetraria nivalis* was 51 % active and 49 % inactive. For NP 44 % were used and for respiration 7 %. The darkly pigmented cortex of *Cetraria islandica* absorbed more heat than the light coloured of *Flavocetraria nivalis* and therefore the WC of *Cetraria islandica* decreased faster. However, dark lichens may absorb heat and consequently increase availability of water by quick melting of freshly fallen snow (Kappen 1988). Periods with continual high hydration sufficient for photosynthesis are often connected with low light intensities. Nevertheless just in these situations the lichens reach high rates of NP. Thus it is to assume that foggy and cloudy days are most important for the CO_2 gain of lichens. There are great differences of the maximal WC measured in the field and in the laboratory. In both cases the maximal WC in the field is twice higher than in the laboratory. Errors in WC determining were possibly caused during rainy periods when water droplets were still adhering to the lichens although they were carefully

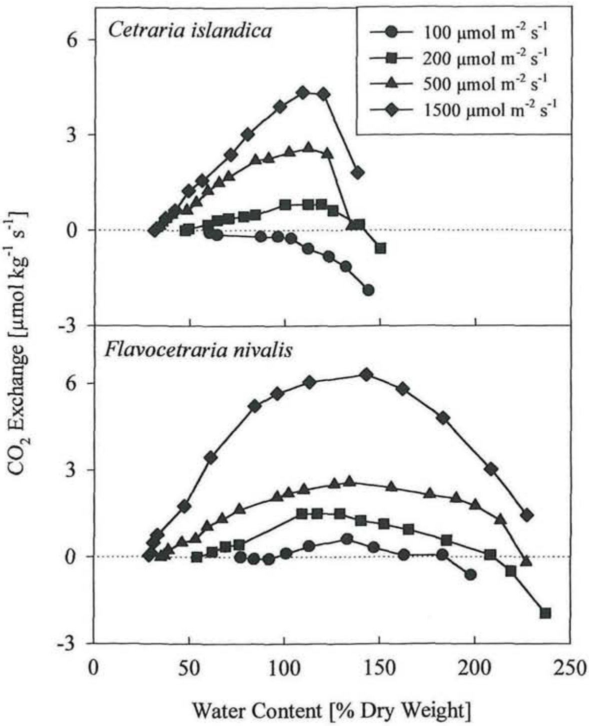


Fig. 6. Relationships between CO_2 uptake (symbols) and thallus water content for *Cetraria islandica* and *Flavocetraria nivalis* at various light intensities and 15 °C in the laboratory.

shaken before weighing. TÜRK 1983 found a maximal WC of *Cetraria islandica* of 245 % and of *Flavocetraria nivalis* of 410 %. These values reached in the laboratory are close to the range of those which are found in the field. SCHIPPERGES & al. 1995 reported from temperate to arctic populations of *Flavocetraria nivalis* maximum thallus WC ranged between 292–398 % according to field measurements and between 284–395 % according to laboratory measurements. Watersaturation of fruticose and foliose lichens are typically between 120–200 % (BLUM 1973). Minimal WC in the range of 8-12 % remained far below the MCP.

Restricted NP with supersaturated thalli (Fig. 6) is caused due to increased CO_2 diffusion resistance of the cortex (LANGE & TENHUNEN 1981, COWAN & al. 1992, GREEN & al. 1994). These reductions of NP are minimized at optimal temperatures and radiation. Maximal dark respiration was reached with full thallus saturation.

Lichens are also able to increase their WC only via watervapour uptake as seen on October 24th (Fig. 4) and 22 % (*Cetraria islandica*) respec-

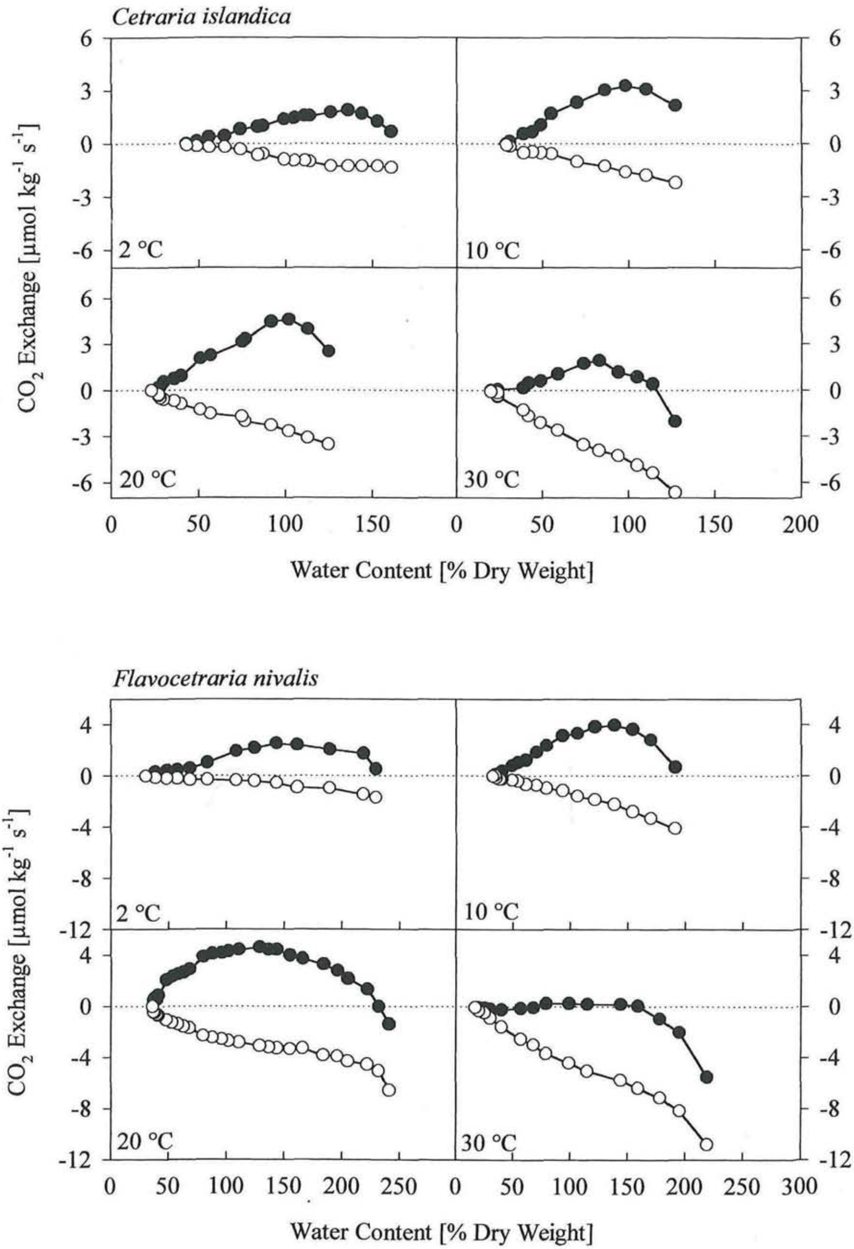


Fig. 7. Relationships between CO_2 uptake (dots), CO_2 release (circles) and thallus water content for *Cetraria islandica* and *Flavocetraria nivalis* at various temperatures and 1000 µmol m^{-2} s^{-1} in the laboratory.

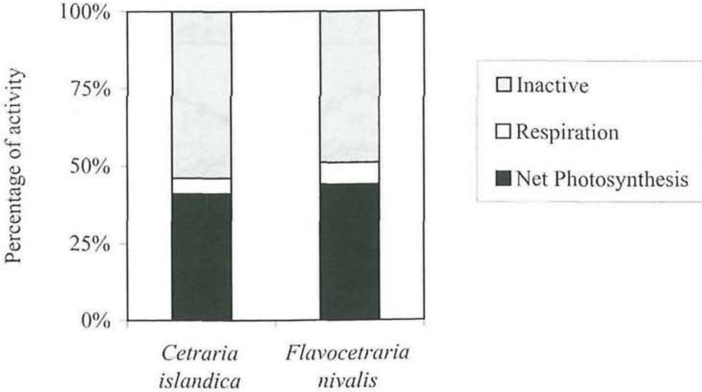


Fig. 8. Amount of activity during the daylight, as a percentage of total observed time, for *Cetraria islandica* and *Flavocetraria nivalis* from August 28th to Sepember 10th and October 21st to October 25th. Black columns: positive net photosynthetic CO_2 uptake; gray columns: metabolic inactivity in the dry state; white columns: respiratory CO_2 release.

tively 36 % (*Flavocetraria nivalis*) of maximal field NP was reached. LANGE & KILIAN 1985 reactivated in the laboratory the photosynthesis of dry lichens by water vapour uptake. The quickness of hydration is dependent to morphological and anatomical characteristics. In comparison with other species, the water vapor reactivation of *Cetraria islandica* was of medium value.

Regarding the light intensity both investigated lichens show typical adaptations to high irradiation. The LCP detected in the laboratory at 15 °C was higher than in the field at 0.5–2.0 °C; thus LCP decreases with decreasing temperature. Differences in LCP is also caused due to higher self shading in the laboratory, because the lichens obtain radiation from above, whereas in the field the thalli get light also from the side. The higher self shading in the laboratory consequently caused a higher LCP. Interspecific differences of LCP between species can influence the CO_2 balance as seen on September 9th. After midday an increase of the cloud-cover reduced drastically the radiation and CO_2 exchange in *Flavocetraria nivalis* turned to respiration while in *Cetraria islandica*, the lichen with the lower LCP, positive NP was detected. This may be an explanation for the observed faster growing of this lichen. Intraspecific variations of the physiology and morphology of populations of *Flavocetraria nivalis* growing from temperate to arctic zones were published by SCHIPPERGES & al. 1995.

The investigated lichens are well adapted to low temperatures. At –8 °C CO_2 assimilation was still detected and even when the lichens were frozen, 24 % (*Cetraria islandica*) respectively 38 % (*Flavocetraria nivalis*) of maximal NP were reached. For subarctic *Flavocetraria nivalis* CO_2 uptake at –20 °C has been reported (KALLIO & HEINONEN 1971). The lowest temperature for CO_2 uptake was –24 °C, recorded for *Stereocaulon alpinum* and *Cladonia alcicornis* (LANGE 1962). Lowest recorded temperature for photosynthetic activity of lichen species measured in the laboratory or in the field was summarized by KAPPEN 1993. Metabolic activity at subzero temperatures has been reviewed by KAPPEN 1993, KAPPEN & al. 1996, KAPPEN & SCHROETER 1997 and SCHROETER 1997.

At 30 °C, highest temperature tested in the laboratory, *Cetraria islandica* was able to reach 40 % of maximal NP. In contrast *Flavocetraria nivalis* did not reach positive NP at this temperature. Also subalpine *Cetraria islandica* and *Flavocetraria nivalis* (TÜRK 1981), arctic *Flavocetraria nivalis* (SCHIPPERGES 1992) and alpine *Umbilicaria cylindrica* (REITER & TÜRK 2000) do not surpass the TCP at 30 °C. The higher upper temperature compensation point of *Cetraria islandica* is a possible explanation for the larger range of the occurrence in different altitudes. *Cetraria islandica* is found from the lowlands up to the nival step in the Alps.

The maximal NP measured in both fruticose lichens corresponds with that reported in the literature. KAPPEN 1988 and LONGTON 1988 have summarized rates of photosynthesis and respiration of alpine and arctic lichens; the photosynthetic capacity decreases with increasing latitude. A review of ecophysiological works on *Flavocetraria nivalis* is given by SCHIPPERGES 1992.

Maximal CO_2 uptake in the field reached 65 % in comparison with those in the laboratory. Thus, optimal combination of WC, radiation and temperature can be established in the laboratory, but optimal conditions do not often exist in the field. Maximal NP depends also on the CO_2 concentration of the air. The partial pressure of CO_2 is lower in the alpine study site than in the laboratory.

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Recensio

LACK H. Walter with MABBERLEY David J. 1999. The Flora Graeca Story. SIBTHORP, BAUER, and HAWKINS in the Levant. – Lex. 8°, XXXII + 327 Seiten, XVII Farbtafeln, 69 Abb., 9 Karten; geb. – Oxford University Press, Oxford, New York, Tokyo. – £ 250,–. – ISBN 0-19-854897-4.

Als der Rezensent das Buch studiert hatte, im Geiste an eine Zusammenfassung dachte und zuletzt noch das Vorwort las, ergab sich, daß es kaum möglich sein dürfte, eine bessere Charakteristik des Werkes zu formulieren, als sie in einem Absatz des Vorwortes auf p. VIII enthalten ist: „Whereas there are several comprehensive publications about the French an Danish expeditions, the journeys of Sibthorp, Hawkins, and Bauer have never been studied in any detail. Based on extensive material,

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