# CO$_2$ Exchange in the Alpine Sedge *Carex curvula* as Influenced by Canopy Structure, Light and Temperature

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**Summary.** The temperature and light responses of CO$_2$ uptake ($F_n$) in the sedge *Carex curvula* were investigated in situ by IRGA technic in the Austrian Central Alps at an altitude of 2,310 m. $F_n$ in *Carex* leaves reaches a maximum of 15.6 mg CO$_2$ dm$^{-2}$ h$^{-1}$ at a leaf temperature of 22.5° C and a quantum flux density larger than 1.0 mmol photons m$^{-2}$ s$^{-1}$ (400–700 nm). A model based on a polynomal regression analysis of the $F_n$ responses and informations about the microclimate and the canopy structure was used to simulate $F_n$ for individual days and for a whole season. It turned out that the major rate limiting factor is the availability of light in the canopy: The calculated photosynthetic yield for a hypothetical optimum season of clear days with fully illuminated leaves and optimum temperature as well as for a typical season with the actual light and temperature conditions in the canopy, shows that insufficient illumination of the leaves accounts for almost 40% reduction of the possible CO$_2$ uptake while suboptimal temperatures cause only a loss of 8%. Half of the light deficit is caused by mutual shading of the leaves. The minor importance of temperature for the annual CO$_2$ uptake results from the fact that temperature adaptation of $F_n$ in this sedge allows optimal utilization of short periods with high light intensity and hence high photosynthetic yield. The weaker the quantum supply the more becomes temperature limiting. This indicates that the length of the growing season is probably less important for the success of this prominent alpine plant than the sum of hours with high radiation.

*List of Symbols*

$I_o$    quantum flux density in a horizontal plane above the plant canopy (μmol photons m$^{-2}$ s$^{-1}$, 400–700 nm)

$I_z$    as $I_o$, but at level $z$ in the leaf canopy

$I_l$    quantum flux density received by a leaf at level $z$ and with leaf inclination $\gamma$ (for diffuse light $I_z = I_l$)

$\beta$    solar elevation angle (°)

$\gamma$    leaf angle to the vertical (°)

$k$    extinction coefficient

LAI    leaf area index

$T_l$    leaf temperature (°C)

$F_n$    rate of net photosynthesis (CO$_2$ uptake; mg CO$_2$ g dry weight$^{-1}$ h$^{-1}$, or mg CO$_2$ dm$^{-2}$ h$^{-1}$, projected leaf area)

$R_d$    rate of dark respiration (mg CO$_2$ g$^{-1}$ h$^{-1}$)

# 1 Introduction

The short and cool growing season in alpine areas of the temperate zone requires particularly adapted plant responses to the environment to gain sufficient carbohydrate to complete the annual phenological cycle and in the case of perennials, to maintain a balanced carbon budget over the years.

Alpine dwarf shrubs, cushion plants and low rosette plants favour the development of a warm microenvironment in their dense leaf canopies (Salisbury and Spomer 1964; Cernusca 1976; Körner and Moraes 1979; Larcher 1980a) and the photosynthetic responses seem to be well adapted to these conditions (Larcher and Wagner 1976; Grabherr 1977; Moser et al. 1977; Larcher 1980a). However no such pronounced positive canopy effects are found in the sparse sedge communities which dominate in the Central Alps above ca 2,200 m, and in which *Carex curvula* is the most important plant species. Although heat accumulation in such a sedge canopy may shortly reach 8 K above ambient air temperature under clear and calm midday conditions, 4 K are usually not exceeded (Cernusca 1977). In contrast values of 10 to 20 K above air temperature were observed frequently in dwarf shrubs and cushion plants.

In this study it was investigated how photosynthesis in Carex curvula responds to the microclimate in the leaf canopy and to which extent are climatic factors limiting CO$_2$ uptake during the short growing season. Together with models for soil respiration and for dark respiration of whole stands (Cernusca and Decker 1977; Decker 1981) this analysis also provides a basis for the estimation of the annual carbon balance.

## 2 Material and Methods

### 2.1 Experimental Site and Plant Material

*Site.* The studies have been conducted in the Austrian Central Alps at 2,310 m above sea level (MaB-station 'Wallackhaus', Hohe Tauern, 47°04′ N, 12°51′ E). The investigated sedge mat (*Caricetum curvulae*, Oberdorfer 1959) is 8–12 cm tall with a leaf area index of phanerogams of 2.3 (Pümpel 1977). Besides *Carex curvula* All. which constitutes about 60% of the above ground phytomass of phanerogams the stand comprises small rosette plants (e.g. *Primula minima* L. and *Hieracium* sp.) and fruticous lichens which cover the ground in the lower 3 cm of the canopy.

*Plant Material.* The rhizomatous sedge *Carex curvula* has shoots, which usually consist of two 'young' leaves and two more rigid 'old' leaves which have emerged a second time from a one year old meristem. In September the above ground green portion of the leaves dies back, but its remainders stay attached to the

**Table 1.** Characteristics of *Carex curvula* leaves. All samples were collected in midsummer. The number of samples for maximum leaf conductance represents the number of clear day courses of conductance from which the absolute maxima were taken for the mean maximum given here. For chlorophyll content random samples with ca 50 leaves each were analysed

| | $n$ | Mean $\pm$ SD |
|---|---|---|
| Specific leaf area (projected) | 68 | $1.12 \pm 0.12$ dm$^2$ g$^{-1}$ |
| Leaf width | 100 | 1.1 $\pm 0.25$ mm |
| Leaf length (green part) | 100 | 55 $\pm 15$ mm |
| Stomata frequency and distribution | 6 | 64 $\pm 14$, only abaxial |
| Maximum leaf diffusive conductance for water vapour (Körner and Mayr 1981, projected leaf area) | 13 | $1.10 \pm 0.30$ cm s$^{-1}$ |
| Chlorophyll content (determined according to the method of Arnon, 1949) | 4 | $3.45 \pm 0.11$ mg g dry weight$^{-1}$ |
| Chlorophyll $a/b$ ratio | 4 | 3.40 |

**Table 2.** Frequency distribution of temperatures during daylight hours ($I_o > 50$ µmol photons m$^{-2}$ s$^{-1}$) in summer 1976. Hourly means of air temperature 2 m above the ground (Weiss 1977) and means and maxima of leaf temperature in the middle of the *Carex* canopy (Seeber 1982). July 1976 was exceptionally warm, August 1976 was cooler than usual

| Temperature (°C) | | | July % | August % | Total % |
|---|---|---|---|---|---|
| $T_{air}$ | $T_l$ | (max) | | | |
| $-2$ to 0 | $-6$ to 0 | $(-)$ | 0.0 | 1.2 | 0.6 |
| 0 to $+2$ | $-2$ to $+1$ | (6) | 4.9 | 2.5 | 3.7 |
| $+2$ to 4 | $+1$ to 4 | (11) | 9.3 | 29.4 | 19.4 |
| 4 to 6 | 4 to 7.5 | (15) | 7.8 | 30.1 | 19.0 |
| 6 to 8 | 7.5 to 11 | (18) | 17.7 | 18.4 | 18.0 |
| 8 to 10 | 11 to 14 | (21) | 22.1 | 14.1 | 18.1 |
| 10 to 12 | 14 to 17 | (23) | 19.1 | 3.7 | 11.4 |
| 12 to 14 | 17 to 20.5 | (25) | 13.2 | 0.6 | 6.9 |
| 14 to 16 | 20.5 to 24 | (26) | 5.9 | 0.0 | 2.9 |
| | | | 100.0 | 100.0 | 100.0 |

below ground portion. In June the two one year old and two new basal leaf meristems become active and within about three weeks the full green leaf area is reestablished. As basal growth continues while leaf tips start to die off when a certain leaf length is reached, the green portions of the leaves are similar in length and age for the main part of the growing season. Leaf characteristics of *Carex curvula* are listed in Table 1. During this investigation 24 shoots have been studied between early July and beginning of September in 1976 and 1977. The shoots remained one to two days in the gas exchange chamber.
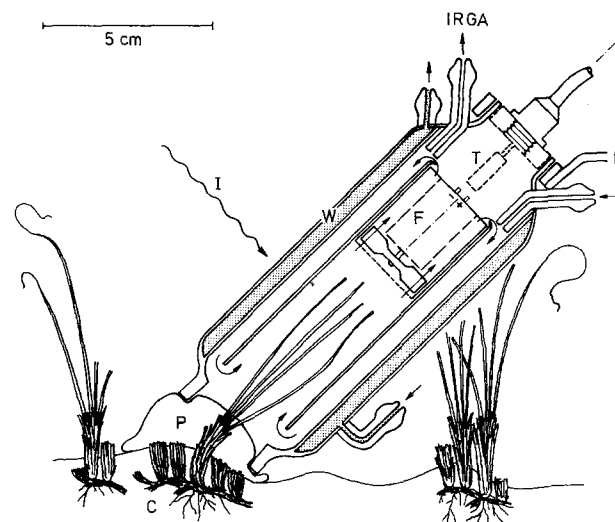
*Climate.* At this site the period without a permanent snow cover lasts only 10 to 15 weeks. Precipitation amounts 1,300 to 2,000 mm a$^{-1}$, with approximately 700 mm falling during the snow free period in summer (Weiss 1980). The annual average of air temperature is $-3°$ C, the mean air temperature between mid June and mid September is $+5°$ C with extremes of $-5$ and $+16°$ C (data from 1976, Weiss 1977). During the same period the leaf temperatures of *Carex curvula* 4 cm above the ground vary between $-6$ and $+24°$ C, with daytime leaf temperatures below $+14°$ C occurring during 80% of all daylight hours because of the frequent occurrence of clouds and fog (Table 2).

*Gas Exchange Measurements.* The $CO_2$ exchange of *Carex curvula* was measured with a mobile field laboratory using a differential infrared gas analyser (UNOR 5, Maihak AG, Hamburg, FRG) in an open system as described in detail by Körner (1977c). The temperature controlled plant chamber is shown in Fig. 1. Its water jacket is connected to a cooler unit and a thermostated water bath. The time lag between changes of $CO_2$ concentration in the plant chamber and steady state IRGA output amounts less than two minutes.

*Illumination.* Leaves and cuvette have been orientated so that direct solar radiation was incident close to right angle throughout



**Fig. 1.** The gas exchange chamber (1.2 mm glass). *F* fan, *W* water jacket, *H* holder, *T* temperature and humidity sensor, *P* plastic silicone rubber, *C* rhizom system of *Carex curvula* with one shoot sealed into the chamber

the day and mutual shading of the leaves was kept as small as possible (Fig. 1). Because of the changing light conditions due to clouds, part of the measurements have been conducted with artificial illumination (metal halogen lamp, Osram HQI-E 400 W). Quantum flux density (400–700 nm) was measured in the direction of the incoming radiation (quantum sensor Li 190 S, Licor, Lincoln, USA). Inside the chamber the quantum flux density was 20% lower than outside. The distribution of light in the chamber was homogenous (no optical refraction patterns).

*Temperature and Humidity.* Because of the narrow leaf size and sufficient ventilation of the chamber ($> 1$ ms$^{-1}$) the leaf temperature was considered to be equal to the air temperature in the chamber. The humidity in the chamber was monitored by an electrolytic sensor (Rotronic PG-7, P. Debrunner, Ebmatingen,

Switzerland) but was not controlled. Usually the vapour pressure deficit in the chamber varied between 2 and 13 mbar. Only when the temperature was raised experimentally above $+25°$ C up to 26 mbar were reached shortly, but stomata of *Carex curvula* did not show distinct responses to low humidity (Körner 1980).

*Data Processing.* A bivariate polynomal regression analysis using the least square method was applied. A third order polynom was used to calculate the response surface of $F_n$ as a function of $T_1$ and $I_1$. As the original data were not distributed entirely uniform in the variable space as it would be desirable (Jarvis 1976) the following additional boundary conditions for the poly-nome were installed: (a) light compensation points between $+1$ and 20° C (from Fig. 2 by linear interpolation between dark respiration and $F_n$ at 100–200 μmol photons m$^{-2}$ s$^{-1}$), and (b) the temperature response curve of $F_n$ at light saturation, calcu-lated separately by a second order polynomal regression for all $F_n$ values obtained above 1,200 μmol photons m$^{-2}$ s$^{-1}$. As Mead and Pike (1975) point out, the validity of such regressions is restricted to the space filled by original data. In the present study the original data cover very well the range of actually occurring temperatures and light conditions in the field. No data are available for conditions with temperatures below $+1°$ C which occur in summer only during 4.3% of the total number of daylight hours (Table 2). Therefore, except for those rare situations, no extrapolations were necessary. Separate regressions for responses of $F_n$ and $R_d$ were used, because a single regression covering the whole $CO_2$ response in light and dark gave lower accuracy in the lower light range (cf. Lechowicz 1978).

## 3 Results

*The variation of $CO_2$ uptake with changes in light intensity ($I_1$) and leaf temperature ($T_1$)* is shown in Fig. 2. Of all data 98% are in the space between the two boundaries, the shape of which indicates the character of the light response of $F_n$. The computed third order polynom for these data of the form

$$z = a + bx + cy + dx^2 + ex + fy^2 + gx^3 + bx^2y + ixy^2 + jy^3,$$

where

$$x = 40^{-1}T_1, \quad y = 2,000^{-1}I_1, \quad z = 18.6^{-1}F_n, \tag{1}$$

has the following coefficients:

| | | |
|---|---|---|
| $a = -0.0601$ | $d = 0.5777$ | $g = -1.7868$ |
| $b = 0.1880$ | $e = 3.7320$ | $h = -1.2852$ |
| $c = 1.6025$ | $f = -3.2141$ | $i = -1.5324$ |
| | | $j = 1.8222$ |

The standard error for the calculated response surface is 1.21 mg $CO_2$ g$^{-1}$ h$^{-1}$. The relative error amounts 13.1%. A scatter plot of the residuals ($F_n$ measured minus $F_n$ predicted, Jarvis 1976) showed that the positive and negative errors are equally distrib-uted each side of zero, thus the function fits well with the data. Using this regression polynom the temperature dependency of $F_n$ at different light intensities was calculated (Fig. 3).

*Light Response of $CO_2$ Uptake.* $F_n$ in Carex curvula is light saturated at $I_1 > 1,000$ μmol photons m$^{-2}$ s$^{-1}$ as in most herba-ceous heliophytes (for data comparison see Larcher 1980 b). Also the large chlorophyll $a/b$ ratio (Table 1) indicates the 'sun leaf' character of the leaves of *Carex curvula*. Similar high saturation quantum flux densities were observed in other herbaceous alpine plant species by Cartellieri (1940), Scott and Billings (1964) and
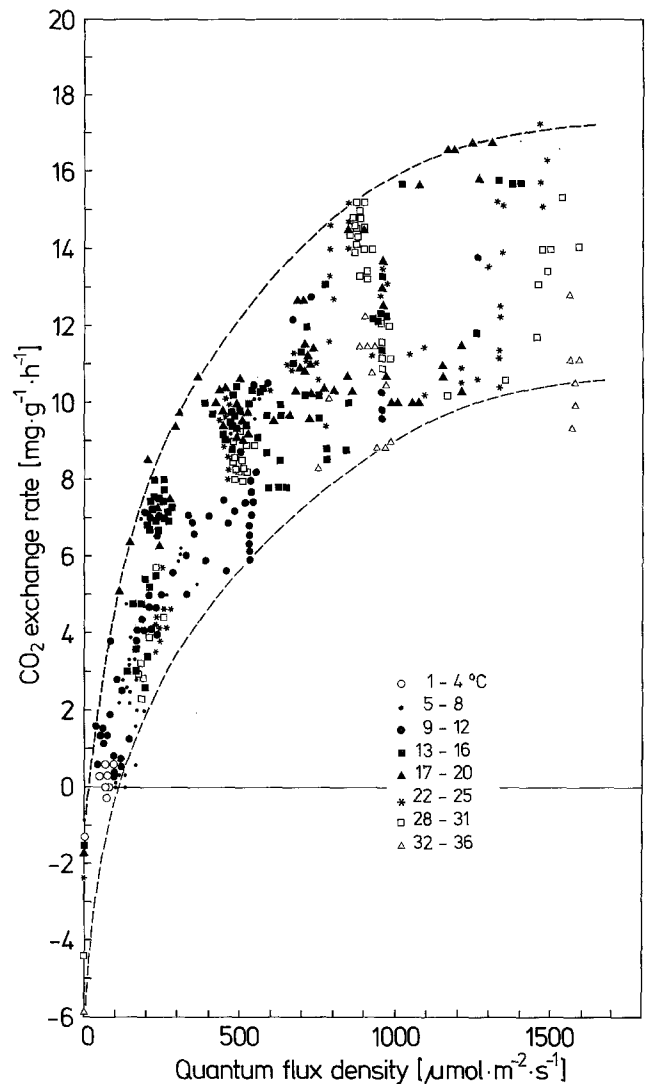


**Fig. 2.** $CO_2$ exchange in *Carex curvula* under various light and tempera-ture conditions in the field. The data points for dark respiration repre-sent mean values for each of the selected temperature classes. All values are steady state readings after at least 15 min of equilibration at a certain combination of light and temperature

Moser et al. (1977), while $CO_2$ uptake in alpine snow tussocks (Mark 1975), small cushion plants in the nival belt (Moser et al. 1977) and deciduous alpine dwarf shrubs (Larcher 1977) is satu-rated at much lower quantum flux densities around 500 μmol photons m$^{-2}$ s$^{-1}$.

*Temperature Response of $CO_2$ Uptake.* As Fig. 3 shows, the tem-perature optimum of $F_n$ shifts from $+14°$ C at 100 μmol photons m$^{-2}$ s$^{-1}$ to $+22.5°$ C at light saturation, which corresponds to the mean maximum leaf temperature on clear summer days (Seeber 1982) and is similar to the average values for herbs of the temperate zone, including many alpine species (e.g. Mooney and Billings 1961; Mooney and Johnson 1965; Johnson and Caldwell 1975; Moser et al. 1977; Larcher 1980a). Grasses and sedges of the arctic tundra show substantially lower tempera-ture optima (10–15° C; Johnson and Caldwell 1975; Tieszen and Wieland 1975; Mayo et al. 1977). *Carex curvula* has a wide range of optimum temperature for $F_n$: Under light saturation 90% of maximum $F_n$ are reached between 16 and 28° C. At
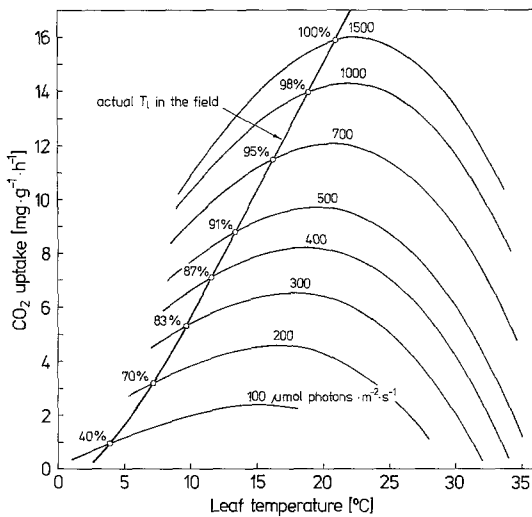
**Fig. 3.** The temperature response of $F_n$ in *Carex curvula* at different quantum flux densities calculated by Eq. (1). The 'actual $T_l$' represents the average temperature observed in the field at each of the selected $I_l$ during July and August (cf. Table 4). The relative $F_n$ reached at these field temperatures is indicated. The maximum $F_n$ at each quantum flux density is set equal to 100%

400 µmol photons m$^{-2}$ s$^{-1}$ 50% of maximum $F_n$ are reached between +3 and 31° C. The temperature limits of $F_n$ have not been studied, but it can be expected from the shape of the temperature responses and from studies in other alpine species including the sedge *Carex firma* (Larcher and Wagner 1976) that the $CO_2$ budget of illuminated leaves is positive at 0° C and that the heat limit of $F_n$ is far beyond the maximum temperatures observed in the field (Table 2).

*Maximum $CO_2$ Uptake.* The average maximum $F_n$ in *Carex curvula* under the given experimental conditions ($305 \pm 5$ µl $CO_2$ l$^{-1}$ or 9.6 µmol l$^{-1}$) reaches 16 mg g$^{-1}$ h$^{-1}$ (extreme 18.6) or 14.4 mg dm$^{-2}$ h$^{-1}$. At 330 µl $CO_2$ l$^{-1}$ the uptake of $CO_2$ will reach approximately 15.6 mg dm$^{-2}$ h$^{-1}$. Maximum $F_n$ (mg dm$^{-2}$ h$^{-1}$) obtained in other herbaceous alpine plant species by Cartellieri (1940), Billings et al. (1966), Johnson and Caldwell (1975), Lloyd and Woolhouse (1976) and Moser et al. (1977) range from 7 to 27 with most values between 12 and 18. Thus the value for Carex curvula holds a middle position. It corresponds also well with data from arctic grasses obtained by Tieszen (1973) where 7 of 9 species ranked between 10 and 20 (mean 14.5). Temperate lowland C-3 grasses show somewhat higher rates ranging from 14 to 27 (mean 20; data from Grace and Thompson 1973, Frank and Barker 1976, Gloser 1976). Although the frequent lack of information about the $CO_2$ concentrations during the experiments reduces the significance of such a comparison, the difference in $F_n$ between lowland and alpine C-3 graminoids of the temperate zone may result from the reduced partial pressure of $CO_2$ at high altitudes (Billings et al. 1961; Tranquillini 1979). Assuming a linear relation between $F_n$ and partial pressure of $CO_2$ in this range of concentrations and a constant volume fraction of $CO_2$ in air, maximum $F_n$ of *Carex curvula* would reach 20.5 mg dm$^{-2}$ h$^{-1}$ at a total pressure of 1,013 mbar. Thus at the same partial pressure gradient of $CO_2$ in air the difference between mean maximum $F_n$ in lowland and alpine graminoids seems to disappear.

*Dark Respiration.* $R_d$ (mg g$^{-1}$ h$^{-1}$) at night amounts 0.5 at 0° C, 0.8 at 10° C and 1.5 at 20° C. $R_d$ measured during the daylight

hours by darkening the cuvette, was up to two times higher than that at the same temperature at night, although equilibration times of one to two hours were allowed. Therefore some of the frequently reported much higher $R_d$ from short term darkening experiments probably cannot be used for the calculation of $R_d$ during the night (at 20° C values between 2 and 5 are reported by Scott and Billings 1964; Mooney and Johnson 1965; Billings et al. 1966). Decker (1981) found similar low $R_d$ for the detached above ground green portion of the total plant cover in which *Carex curvula* dominates (1.65 mg g$^{-1}$ h$^{-1}$ at 20° C). Compared with other herbaceous plants $R_d$ in *Carex curvula* is quite low. The values are more close to those known from evergreen plants than from herbs and deciduous woody plants (Larcher 1980b). Decker (1981) also found that root respiration in this sedge mat is lower than in other graminoid systems. The respiratory loss of $CO_2$ by leaves during one night (mean $T_l = +4°$ C) reaches approximately 5 mg g$^{-1}$ and thus amounts 1/12–1/24 of the diurnal $CO_2$ uptake on overcast and clear days (cf 4.2).

## 4 Discussion

It results that the predominant alpine sedge *Carex curvula* is a typical herbaceous heliophyte with photosynthetic responses of individual leaves not much different from those known from other graminoid plant species both in lowland and alpine areas. In the following discussion the effect of the environmental conditions in the field on the actual $CO_2$ uptake will be considered.

Particular attention will be directed to the light climate in the canopy, as the temperature response of $F_n$ shows a wide optimum range and hardly limits $CO_2$ uptake at a given quantum flux density (Fig. 3). Water shortage has been shown to play a minor role at the study site for the control of gas diffusion of *Carex curvula* (Körner 1977b; Körner et al. 1980; Körner and Mayr 1981). Water has been found to be sufficiently available throughout the season and stomatal diffusive conductance varied usually only between 0.6 and 1.1 cm s$^{-1}$ in three successive seasons (1976–1978). As a result of the narrow leaf size, of low LAI and the regularly high wind speed also the aerodynamic resistance is rather low in this sedge community (Körner 1977a).

### 4.1 Canopy Structure and Light Climate

The distribution and orientation of the green part of the leaves of *Carex curvula* and the light extinction in the canopy are described by Cernusca (1977), Pümpel (1977) and Seeber (1982). From these studies it can be concluded that a leaf layer 4 cm above soil surface is most representative for the total canopy of green *Carex* leaves. 61% of the total green leaf area of *Carex curvula* are between 2 and 6 cm, with an average portion of 44% above (4–12 cm) and 56% below (0–4 cm) the 4 cm level. Therefore the following considerations are referred to this stratum. The mean total projected leaf area above 4 cm amounts 1.35 m$^2$ m$^{-2}$ including 0.38 m$^2$ m$^{-2}$ green and 0.97 m$^2$ m$^{-2}$ dead leaves.

For the description of the light climate in the canopy under overcast conditions (diffuse radiation) the equation of Monsi and Saeki (1953) was applied:

$$I_l = I_z = I_o \cdot e^{-k \cdot LAI_z}. \tag{2}$$

Cernusca (1977) showed that this function is valid for this *Carex curvula* canopy. The extinction coefficient $k$ for the total canopy is 0.34 and for the part of the canopy above 4 cm it is 0.40

**Table 3.** The light interception of leaves of *Carex curvula* during a clear day in midsummer. The extinction coefficient $k$ is obtained from Seeber (1982), the ratio diffuse/direct radiation as well as the mean midday quantum flux density for overcast conditions at this altitude were obtained from Dirmhirn (1964). Further information in the text

| Solar time | | Solar angle | $k$ | $I_o$ | $\dfrac{\text{diffuse}}{\text{direct}}$ | $I_1$ $(\gamma=33°)$ |
|---|---|---|---|---|---|---|
| 06.00 | 18.00 | 17° | 1.08 | 230 | 0.37 | 120 |
| 08.00 | 16.00 | 37° | 0.63 | 1,120 | 0.11 | 641 |
| 10.00 | 14.00 | 56° | 0.34 | 1,850 | 0.08 | 816 |
| 12.00 | | 65° | 0.25 | 2,140 | 0.07 | 874 |
| 12.00 (overcast sky) | | | 0.40 | 790 | 1.00 | 460 |

(higher portion of horizontal, dead leaf curls in the uppermost stratum). It results that under diffuse light conditions 58% of the incoming light penetrates the upper part of the canopy and reaches the 4 cm stratum.

Under clear sky conditions direct beam–leaf interactions and a variable portion of diffuse radiation which is intercepted independently of leaf angle have to be considered separately. Although clear sky conditions are rare at this site they may be of importance for the annual $CO_2$ uptake. Therefore it was tried to estimate the extent to which leaf angle in *Carex curvula* influences $CO_2$ uptake. Pümpel (1977) showed that most leaves in this sedge are inclinated by 33° to the vertical. With symmetrical azimuthal leaf orientation and various solar elevations the quantum intercept of *Carex* leaves was calculated applying the cosine correction (Ross 1975). Table 3 shows the estimated mean light intercept during a clear day in midsummer. It turns out that the mean quantum flux density at the leaf surfaces undergoes surprisingly small variation between 8.00 and 16.00 h. Mainly as a result of changing sun–leaf angles $I_1$ remains within 641–874 µmol photons $m^{-2}\,s^{-1}$ while $I_o$ varies between 1,120 and 2,140 µmol photons $m^{-2}\,s^{-1}$. This also indicates that light saturation of $F_n$ is not reached under such conditions and relatively high quantum flux density is reached allready early during the day. This may be important as morning hours are usually less cloudy then the noon hours and also the extinction coefficient for direct radiation is much higher in the morning (Table 3). A comparison of two simplified leaf orientation models showed that a vertical leaf model ($\gamma=0°$) yields reasonable results (deviation from the realistic model by ±8%) whereas a horizontal leaf model ($\gamma=90°$) can not be accepted under clear sky conditions (−56 to +74%).

### 4.2 $CO_2$ Uptake on Overcast and Clear Summer Days

Under average overcast conditions ($I_o$ from Dirmhirn 1964, $T_1$ from Seeber 1982) the diurnal course of $F_n$ calculated by equations 1 and 2 shows a triangular shape with a short midday peak of 7 mg $CO_2$ $g^{-1}\,h^{-1}$ and a continuous, nearly linear increase in the morning and decrease in the afternoon. The total estimated uptake during the daylight hours amounts 62 mg $g^{-1}\,h^{-1}$. If calculated for normal overcast field conditions with short term variation of light intensity similar results are obtained: On July 7, 1977, a typical overcast day a total uptake of 56 mg $g^{-1}\,h^{-1}$ results.

The $CO_2$ uptake for clear days has been estimated on the basis of the assumptions for the interception of direct beam in the canopy in 4.1 ($I_o$ from Weiss 1977, $T_1$ and $k$ from Seeber 1982). As a first approximation this simple method yields a daily $CO_2$ uptake under clear sky conditions of 122 mg $CO_2$ $g^{-1}$,
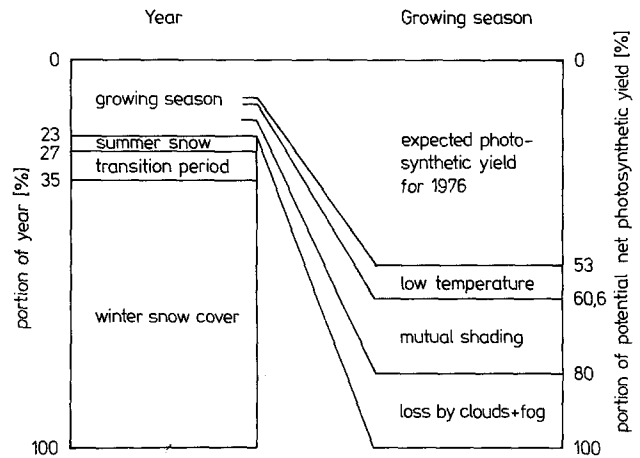


**Fig. 4.** The limitation of $CO_2$ uptake of *Carex curvula* at its natural alpine habitat. The potential net photosynthetic yield under hypothetically optimal climatic conditions is set equal to 100%. The expected net photosynthetic yield for 1976 corresponds to the sum given in Table 4. Further explanation in the text

which is about two times the $CO_2$ uptake during an overcast day. As the light response of $F_n$ is not linear over the range of light intensities in the field, the use of a uniform horizontal distribution of light intensity tends to overestimate $F_n$. This error is smallest ($<10\%$) at noon at high $I_o$ and small $k$ but may be substantially during early and late hours of the day. Thus for a more precise calculation for the whole leaf canopy a separate consideration of sunflecks and shaded leaf areas in different canopy layers and leaf angle classes would be required (Norman 1980).

The calculated course of $F_n$ shows remarkably low variation between 8.00 and 16.00 h ($12\pm1$ mg $CO_2$ $g^{-1}\,h^{-1}$). This results from the relatively uniform quantum interception because of changing leaf–light incidence angles (4.1). Unpublished studies with the climatized Siemens SIRIGOR gas exchange system in sections of *Carex* canopy in the field yielded the same result and thus seem to support the value of the above estimate.

### 4.3 Estimation of the Annual Photosynthetic Yield

To demonstrate the influence of light, canopy structure and temperature on the annual $CO_2$ uptake of *Carex curvual* equations 1 and 2 were used to compute the total $CO_2$ uptake for the actual climatic situation of one year (1976) as well as for a hypothetical growing season with optimal climatic conditions. The application of equation 2 also for clear sky conditions leads to an overestimation of light interception and hence of $F_n$ by 7 to 30% depending on solar elevation (no cosine correction, cf 4.1). As such periods represent less than 1/4 of all daylight hours the final error is probably less than 10%.

During 237 days or 65% of the considered year the ground was covered by a permanent snow cover (Fig. 4). The remaining period of 128 days (35%) has been divided in three portions: (1) the period shortly after snow melt during which *Carex* leaves are still not emerged or emerging together with the period at the end of the season during which leaves decay (transition period, 8%) and (2) periods during which plants are covered by snow at daylight hours in summer (4%) and (3) the period defined as 'growing season' which lasts 84 days (23% of the year) and comprises 1045 h with $I_1$ higher than the light compensation point of $F_n$. Table 4 shows the frequency distribution of $I_o$ during

**Table 4.** Frequency distribution of quantum flux density $(I_o)$ between June 15 and September 15, 1976. $I_o$ was calculated from hourly means of global radiation listed by Weiss (1977) using an empirical conversation factor determined in the field end of July. Numbers in brackets indicate the absolute and relative frequency for continuous clear sky conditions (potential $I_o$). $CO_2$ uptake (mg $CO_2$ g$^{-1}$) was computed using equation 1 and 2. $T_1$ was obtained from Seeber (1982) using the function $T_1 = 0.0136 I_o + 2.0$ $(r = 0.90)$

| $I_o$ | Frequency | | $CO_2$ uptake | |
|---|---|---|---|---|
| | absolute h | relative % | | |
| 50– 250 | 260 (142) | 24.9 (13.6) | 225 | |
| 250– 500 | 183 (86) | 17.5 (8.2) | 673 | 26.4% |
| 500– 750 | 164 (78) | 15.7 (7.5) | 1,153 | |
| 750–1,000 | 93 (78) | 8.9 (7.5) | 896 | |
| 1,000–1,250 | 86 (86) | 8.2 (8.2) | 1,005 | 39.4% |
| 1,250–1,500 | 87 (92) | 8.3 (8.8) | 1,167 | |
| 1,500–1,750 | 66 (114) | 6.3 (10.9) | 964 | |
| 1,750–2,000 | 54 (142) | 5.2 (13.6) | 847 | 34.2% |
| 2,000–2,500 | 52 (228) | 5.0 (21.8) | 844 | |
| | 7,774 | 100.0% | | |

this period and the estimated annual photosynthetic yield for different classes of $I_o$. To illustrate the influence of the microclimate, $I_1$ and $T_1$ were changed stepwise from hypothetically optimum conditions to the real conditions in the field. The result of this analysis is shown in Figure 4. The net photosynthetic yield for 1045 h during about 12 weeks with clear sky but normal astronomic change of light intensity during the day (Table 4) and optimum leaf temperatures was set equal to 100%. In the first step actual values for $I_o$ but still optimum temperatures were applied to indicate the losses caused by overcast sky. The influence of mutual shading of the leaves is shown in the next step, where the reduction of $I_o$ by light extinction in the canopy was considered (Eq. 2). Finally optimum temperatures were substituted by the actual leaf temperatures in the field. With these conditions the resultant total photosynthetic yield in 1976 amounts approximately 7.8 g $CO_2$ g$^{-1}$ dry weight (Table 4) or 53% of the yield computed for a hypothetically optimum season. Insufficient illumination of the leaves accounts for nearly 40% and suboptimal temperatures for about 8% reduction of the potential yield. Thus the availability of photons in the canopy is the major rate limiting factor. Half of the loss due to insufficient light in the canopy results from mutual shading (19.4%). For a dense alpine *Loiseleuria* dwarf shrub canopy Grabherr and Cernusca (1977) estimated a loss by 27%.

Another important point can be seen in Table 4: During only 172 h or 16.5% of all daylight hours of the season with $I_o > 1,500$ µmol photons m$^{-2}$ s$^{-1}$ 34.2% of the estimated annual $CO_2$ uptake occurs. In contrast, the total contribution of daylight hours with $I_o < 750$ µmol photons m$^{-2}$ s$^{-1}$ which are 607 h or nearly two thirds of all daylight hours amounts only 26.4% of the annual yield. Thus short periods with strong radiation are far more important for the annual $CO_2$ uptake of *Carex curvula* than the sum of the prevailing periods with weak light and low temperature.

With respect to the low leaf area index and the low ambient temperatures at this alpine habitat one would expect that suboptimal temperatures play a major rate limiting role. Surprisingly this is not the case. The relative importance of the light and temperature factor for the annual $CO_2$ uptake in *Carex curvula* is similar to that observed by Schulze (1970) in a deciduous

beach forest at low altitude. This results from the fact that in the field suboptimal temperatures restrict $CO_2$ uptake of *Carex curvula* only when the light conditions are very poor and allow small $F_n$. Under strong radiation the observed moderate heat accumulation in the leaf canopy is allready sufficient for optimum photosynthetic yield.

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