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Environmental Control of Carbon Dioxide Gas Exchange in Needles of a Mature *Pinus cembra* Tree at the Alpine Timberline During the Growing Season

By

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With 4 Figures

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Summary

Wieser G. 2004. Environmental control of carbon dioxide gas exchange in needles of a mature *Pinus cembra* tree at the alpine timberline during the growing season. – Phyton (Horn, Austria) 44 (1): 145–153, with 4 figures. – English with German summary.

Seasonal courses of foliage CO_2 gas exchange were measured in the upper sun and the lower shade crown of an adult *Pinus cembra* tree at the alpine timberline during the growing season 2002. Although photosynthetic photon flux density was significantly higher in the upper than in the lower crown daily mean net CO_2 uptake did not differ significantly within the tree and was at an average only 8 % higher in the upper than in the lower crown. Under the prevailing climatic conditions in the timberline ecotone lack of light was the dominating factor limiting carbon gain during the growing season. Data presented in this study combined with data obtained for the winter time (Wieser 1997) allowed the calculation of an annual carbon gain of the foliage of about 2.76 g CO_2 per g needle dry weight.

Zusammenfassung

Wieser G. 2004. Der Einfluss von Umweltfaktoren auf den CO_2 Gaswechsel der Nadeln einer erwachsenen Zirbe an der Waldgrenze während der Vegetationsperiode.

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– Phyton (Horn, Austria) 44 (1): 145–153, 4 Abbildungen. – Englisch mit deutscher Zusammenfassung.

An einer erwachsenen Zirbe an der alpinen Waldgrenze wurde während der Vegetationsperiode 2002 der saisonale Verlauf des CO_2 Gaswechsels von Nadeln in der oberen Sonnen- und der unteren Schattenkrone gemessen. Obwohl die Lichtintensität in der oberen Krone wesentlich stärker als im unteren Kronenbereich war, zeigten sich keine signifikanten Unterschiede in der CO_2-Aufnahmerate innerhalb der Baumkrone. Diese war in der oberen Sonnenkrone durchschnittlich 8% höher als in der Schattenkrone. Unter den klimatischen Bedingungen an der alpinen Waldgrenze war während der Vegetationsperiode der Kohlenstoffgewinn vor allem durch Lichtmangel begrenzt. Die in dieser Arbeit vorgestellten Daten in Verbindung mit früheren Ergebnissen aus dem Winterhalbjahr (WIESER 1997) ergaben einen jährlichen Kohlenstoffgewinn der Nadeln von 2.76 g CO_2 pro g Nadeltrockengewicht.

Introduction

Evergreen conifers are the most common trees at the alpine timberline, an ecotone with strong seasonal changes in climate. Seasonal variation foliar carbon dioxide gas exchange at the alpine timberline has been attributed to seasonal changes in climate. Low temperatures and short vegetation periods limit carbon gain and even may prevent a positive carbon balance throughout an entire year at high elevations (TRANQUILLINI 1979, KÖRNER 1998). However, along an altitudinal gradient within the alpine timberline ecotone BERNOULLI & KÖRNER 1999 found no correlation between total tree biomass and altitude in equal aged trees, which casts doubt on the carbon limitation hypothesis of treeline formation at the alpine timberline (KÖRNER 1998).

Foliar CO_2 gas exchange of adult *Pinus cembra* trees has been investigated using cut twigs under laboratory conditions (CARTELLIERI 1935, PISEK & WINKLER 1958) and in situ during the cold season (WIESER 1997), but there is little information on seasonal variations in net photosynthesis and dark respiration of alpine timberline trees under field conditions during the growing season. Therefore, it was the aim of this study to examine the seasonal changes and environmental constraints in foliar CO_2 gas exchange of an adult subalpine *Pinus cembra* tree in situ under field conditions and to estimate the annual carbon balance of the foliage.

Material and Methods

The study was carried out on a mature 7-m high free standing cembran pine (*Pinus cembra* L.) tree growing on a haplic podzol (WIESER 2004) on a south-west slope at 1950 m a.s.l. near the Klimahaus Research Station on Mt. Patscherkofel (47° N, 11° E) south of Innsbruck, Austria. The field site is characterized by a cool subalpine climate with low temperatures, the possibility of frost in all months and a continuous snow cover from October until May. Meteorological data recorded from the weather station at the study site show a mean annual temperature of 2.4 °C and a mean annual precipitation is 950 mm. Measurements were carried out throughout May 16 to November 11, 2002.

Scaffolding provided access to the crown. CO_2 gas exchange of the last tree flushes was measured continuously by tracking ambient climatic conditions with two climate-controlled chambers (Walz, Effeltrich, Germany, see KOCH & al. 1968) as described previously by on south and north-east exposed branches in the upper sun- (5.5 m above ground) and the lower shade-crown (2 m above ground), respectively.

CO_2 concentration was measured using an infrared gas analyzer (6262, Li-Cor, Inc. Lincoln, Nebraska) in the differential mode and the flow rate of the corresponding air streams were monitored with an electronic mass flow-meter (Tylan, Eching, Germany). The gas streams of the two chambers were measured alternately by means of a solenoid-based, gas-switching system; each chamber being sampled for 3 min intervals with the first two minutes being ignored in order to allow a total flushing of the gas analyzer. Air temperature was measured with 100Ω platinum resistance thermometers, absolute humidity with dew-point mirrors (Walz, Effeltrich, Germany), and irradiance, with a LI-109 PAR quantum sensors (Li-Cor, Inc. Lincoln, NE).

All the data were transmitted to an AM416 multiplexer (Campbell Scientific, Ltd, Shepshed, U.K.) and recorded with a Campbell CR10 data logger, programmed to record 30-min means. The data logger also controlled the switching of the solenoids. CO_2 gas exchange data were based on needle dry weight or total needle surface area estimated by the glass bead technique (THOMPSON & LEYTON 1971).

Analysis of data was based on daily and half-hour means.

Results and Discussion

The present study focused on the effects of crown position on the CO_2 gas exchange of *Pinus cembra* needles. The needles studied differed mainly with respect to 100-needlle dry weight (Table 1), while the specific leaf area was not affected by crown position (Table 1). Photosynthetic capacity (i.e., maximum photosynthetic rate at ambient CO_2, A_{max}; LARCHER 1994) was slightly higher in the lower than in the upper crown, while the opposite was found for night-time dark respiration rate at 10 °C (R_{10}) (Table 1).

Table 1. 100-needle dry weight, ratio of total leaf area to leaf dry mass (= specific leaf area), photosynthetic capacity, and night time dark respiration of current to two-year old needles in the upper sun and lower shade crown of an adult *Pinus cembra* tree.

	Upper sun crown	Lower shade crown
100-neeedle dry weight (g)	2.30 ± 0.67	1.68 ± 0.17
Specific leaf area (cm^2 g^{-1})	61.3 ± 3.8	66.7 ± 2.7
Photosynthetic capacity		
(μmol m^{-2} s^{-1})	4.47 ± 0.2	4.61 ± 0.11
(mg g_{dw}^{-1} h^{-1})	4.35 ± 0.02	4.88 ± 0.12
Night-time respiration rate at 10 °C		
(μmol m^{-2} s^{-1})	0.31 ± 0.07	0.22 ± 0.07
(mg g_{dw}^{-1} h^{-1})	0.30 ± 0.07	0.24 ± 0.07

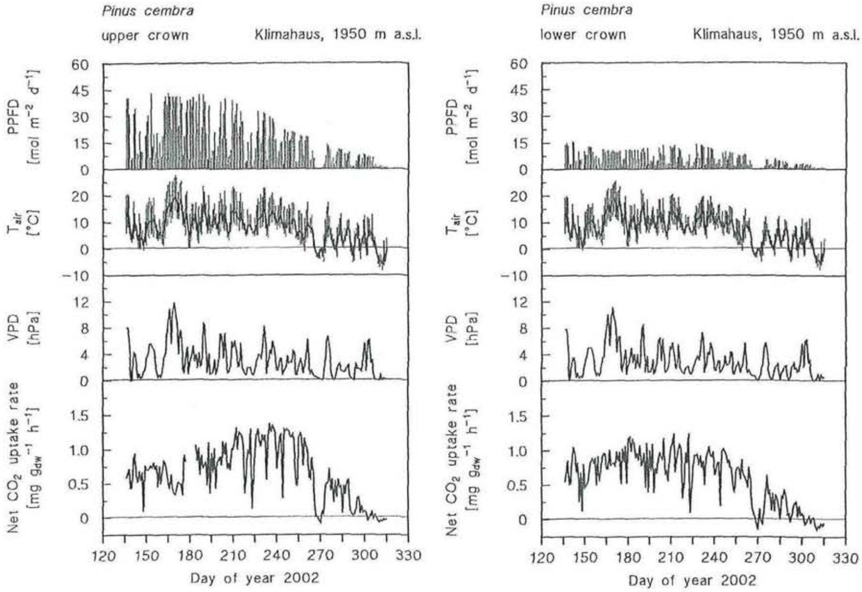

Fig. 1. Seasonal courses of daily sum of photosynthetic photon flux density (PPFD), daily mean air temperature (T_{air}), daily mean vapour pressure deficit (VPD) and daily mean net CO_2 uptake rate of current to two-year old needles in the upper (left) and lower crown (right) of an adult *Pinus cembra* tree between May 16 and November 11, 2002. Vertical bars indicate the daily maximum and minimum T_{air}.

Similar differences in A_{max} and R_{10} between sun and shade needles in cembran pine were also obtained previously by PISEK & WINKLER 1958 when working with detached shoots. In an open high elevation *Pinus canariensis* stand in Tenerife, Canary Islands, PETERS 2001 also failed to find significant differences in A_{max} between the upper and the lower canopy. These findings from open canopies are in contrast to observations in trees growing in relatively dense stands below the *forest line* (i.e. the upper limit of a continuous forest canopy). In temperate (MATYSSEK & SCHULZE 1988), boreal (DANG & al. 1997), montane (HOLLINGER 1989), and Mediterranean (GONZALES-RODRIGUEZ & al. 2001) forest ecosystems net photosynthetic capacity is greatest in the upper part of the crown and declines in parallel with irradiance toward the lower crown.

The seasonal patterns of environmental parameters were representative for the climatic conditions trees experience in the timberline ecotone of the central Tyrolean Alps (Fig. 1). Although photosynthetic photon flux density was significantly higher in the upper than in the lower crown, air temperature and vapour pressure deficit did not differ significantly with respect to canopy position (Fig. 1).

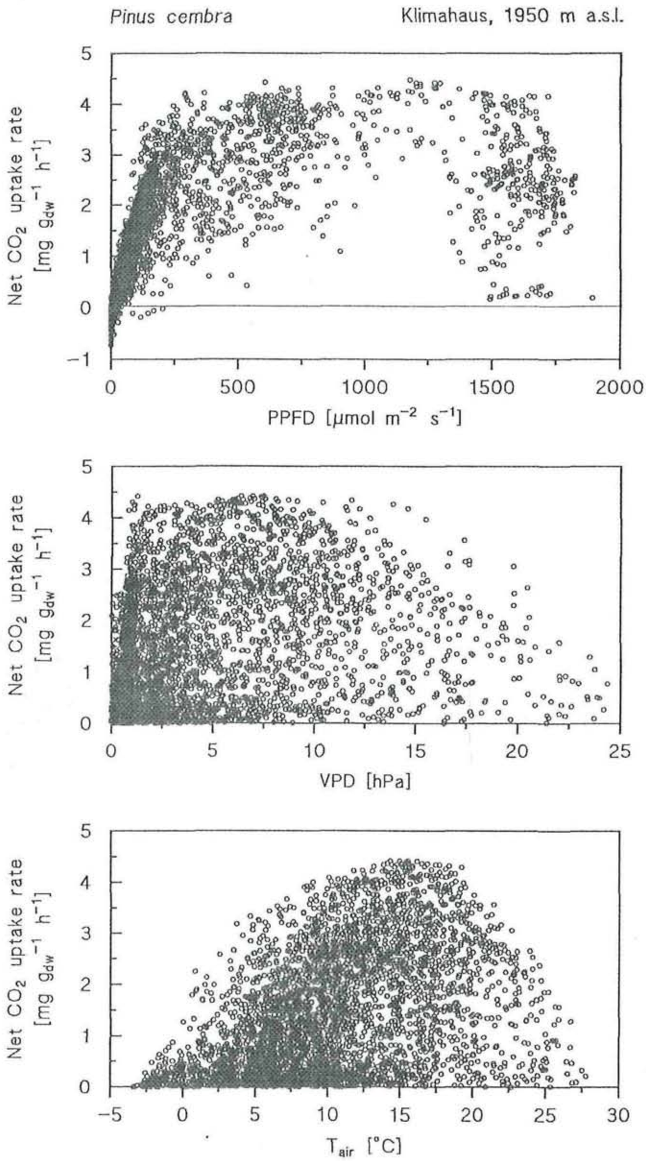

Fig. 2. The relationship between net photosynthesis of current to two-year old *Pinus cembra* needles and photosynthetic photon flux density (PPFD),vapour pressure deficit (VPD), and air temperature (T_{air}).

Seasonal trends in net CO_2 uptake rate generally followed seasonal trends in environmental parameters (Fig. 1). Within the tree, daily mean carbon gain increased till the end of July and reached maximum values in August (Fig. 1). The fall decline was coincident with seasonal trends in day length, irradiance, and temperature (Fig. 1) as also observed previously (WIESER 1997). The magnitude of daily mean net CO_2 uptake however, did not differ significantly within the tree and was at an average 8 % higher in the upper than in the lower crown.

A further analysis of half-hour means confirmed, that there also were no within tree differences in the response of net photosynthesis and dark respiration to photosynthetic photon flux density, vapour pressure deficit, and air temperature. (Fig. 2 and 3). During the growing season lack of light was the most important factor limiting net photosynthesis at (Fig. 2).

During the 2575 daylight hours during the study period photosynthetic photon flux density (PPFD) was below light saturation (<than 650 µmol m^{-2} s^{-1}; Fig. 2) for approximately 40 %. And supra-optimal for further 18%, because high PPFD in the field is generally coupled with high temperature and a high vapour pressure deficit (VPD). Under such conditions VPD indirectly limited CO_2 uptake, because a feed forward response to humidity causes leaf conductance in *Pinus cembra* to decline with increasing evaporative demand (WIESER & al. 2000). This reduction in stomatal conductance limits the diffusion of CO_2 into the needles and hence net photosynthesis also declines with increasing VPD (Fig. 2). The thermal limitation of net photosynthesis by contrast, is relatively unimportant during the growing season because the temperature response curve of net photosynthesis is relatively wide and net photosynthesis operates at more than 90% of its maximum at a temperature range between 7.5 and 19 °C (Fig. 2). Furthermore, the temperature optimum for carbon uptake has been shown to shift with irradiance towards lower values when PPFD is low and towards higher values when PPFD is high (PISEK & WINKLER 1958, PISEK & al. 1969, WIESER 1997). The high and low temperature compensation points of carbon uptake were 27.7 and –3.4 °C, respectively (Fig. 2), while night time dark respiration could be demonstrated down to –7.9 °C (Fig. 3). During the cold season however, low temperatures are the main preconditioning environmental factor limiting foliar gas exchange in *Pinus cembra* at the alpine timberline (WIESER 1997).

Assuming that both locations measured are representative for the spatial variability within the entire tree, gas exchange data from the upper and the lower crown (Fig. 1) were weighted equally and combined with data measured previously on the same tree during the cold season (WIESER 1997) in order to estimate the annual time course of daily total net photosynthesis, daily total night-time respiration and the annual carbon balance of the foliage. Generally, daily total photosynthetic production is positive

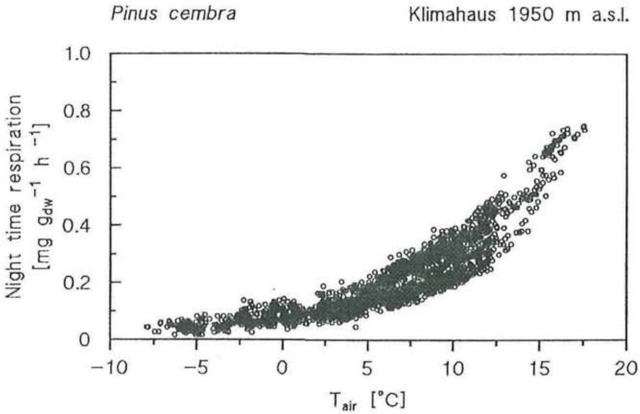

Fig. 3. The relationship between night time (dark) respiration of current to two-year old *Pinus cembra* needles and air temperature (T_{air}).

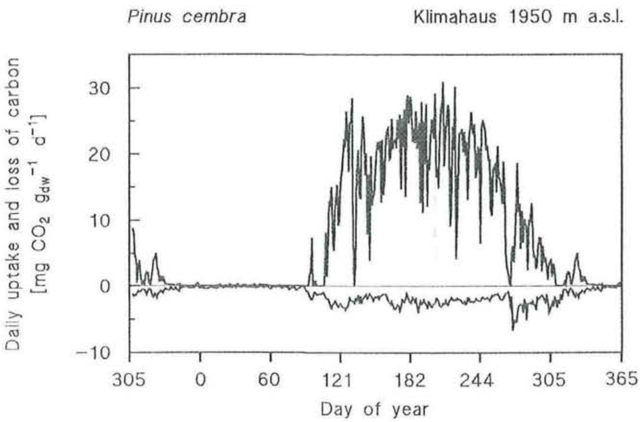

Fig. 4. Seasonal variation in daily total uptake and loss of carbon in current to two-year old *Pinus cembra* needles.

from April till mid November and negative throughout the cold season (Fig. 4).

At the alpine timberline total annual carbon uptake of *Pinus cembra* needles is about 3.3 g CO_2 per g needle dry weight. The total amount of carbon lost by the needles due to night-time respiration and respiratory losses during the winter were about 0.5 g CO_2 per g needle dry weight. Thus, the total annual carbon gain of the foliage is 2.8 g CO_2 per g needle dry weight (Table 2). Once biomass and woody tissue respiration data become available it will be possible to calculate the annual whole-tree car-

Table 2. Annual foliage carbon balance of current to two-year old *Pinus cembra* needles

	($mg\ CO_2\ g\ dw^{-1}$)
Total annual net photosynthesis	+ 3314
Total night-time respiration	– 522
Winter respiration	-31
Annual total CO_2 balance	+ 2761

bon balance. Since a positive foliage carbon balance is necessary for maintenance and growth of the folaiage and woody tissues such data might also help explain the upper elevational limit of tree life.

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