Net Ecosystem Carbon Dioxide Exchange Dynamics in a *Pinus cembra* Forest at the Upper Timberline in the Central Austrian Alps

By

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K e y   w o r d s : Net ecosystem carbon uptake, ecosystem respiration, net ecosystem production, gross primary production, carbon sequestration, cembran pine, high elevation forest, timberline ecotone.

S u m m a r y

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We studied net ecosystem carbon exchange dynamics in a cembran pine (*Pinus cembra* L.) forest ecosystem at the timberline ecotone of the Central European Alps from October 7, 2001 throughout January 21, 2003. Chamber measurements of CO_2 gas exchange of the foliage, woody tissue respiration, and soil surface CO_2 efflux were used to identify the contribution of these components to the net ecosystem CO_2 exchange. We scaled these measurements to the ecosystem and computed the annual total of net ecosystem carbon sequestration and total ecosystem respiration.

Seasonal variations in net ecosystem carbon exchange dynamics were primarily controlled by the prevailing temperature and irradiance. Annual net primary production estimated for 2002 was 1610 g C m^{-2} y^{-1} and total ecosystem respiration was 1247 g C m^{-2} year^{-1}. Annual carbon efflux from the foliage, branches, stems, coarse roots, and the soil surface was 273, 846, 45, 50, and 33 g C m^{-2} year^{-1}, respectively. Net ecosystem production was 363 g C m^{-2} year^{-1}, leading to a ratio of net ecosystem production to gross primary production of 0.23, consistent with values reported for temperate coniferous forest ecosystems, but higher than values reported for boreal coniferous forests. Due to low soil temperature and supra-optimal soil water availability soil surface carbon efflux was relatively low and contributed to only 3% to total ecosystem respiration. Nevertheless, our data indicate that timberline associated *Pinus cembra* forest ecosystems in the Central Austrian Alps act as relative powerful carbon sinks.

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Introduction

The carbon (C) cycle of terrestrial ecosystems, especially forests, has become a focus of climate change research because of their importance for the global C balance (IPCC 2000). Net ecosystem production (NEP; = net C gain or C sequestered) is the small difference between or gross primary production (GPP) and total ecosystem respiration (ER; i.e. the sum of autotrophic and heterotrophic respiration). On an annual basis undisturbed forest ecosystems generally show a small net C gain and data published for 15 European forest ecosystems show a significant decline in NEP with increasing latitude (VALENTINI & al. 2000) clearly indicating that the length of the growing season and hence also temperature strongly affects NEP.

C fluxes for high elevation forest ecosystems have only been investigated in the Snowy Mountains, Wyoming (ZELLER & NIKOLOV 2000) and in the Front Range, Colorado, USA (MONSON & al. 2002). However, there is lack on information on the C exchange of forest ecosystems in the timberline ecotone of the Central European Alps, an ecotone where the assimilatory period is significantly restricted by low temperature, while respiratory processes continue throughout the year (HAVRANEK 1981, TRANQUILLINI 1979, HÄSLER 1994, WIESER 1997, 2004a,b, WIESER& BAHN 2004). Therefore, it was the objective of this study to provide a quantitative assessment of the seasonal dynamics and annual totals of key ecosystem C fluxes in a *Pinus cembra* forest at the alpine timberline.

Material and Methods

Study site and plant material

The study was conducted in a 80 to 100 year-old *Pinus cembra* stand near the Klimahaus Research Station on Mt. Patscherkofel near Innsbruck, Austria (47°N, 11°E; 1950 m a.s.l.) from October 7, 2001 throughout January 21, 2003. The stand density was 1038 trees ha^{-1} and the basal area was 9.5 m^2 ha^{-1}. Characteristics of the sample plot are given in Table 1.

The field site is characterized by a cool subalpine climate with low temperatures and the possibility of frost in all the months. The 40 years of meteorological data recorded at the weather station at the study site showed a mean annual precipitation of 950 mm with the majority falling during the growing season between May and October. The mean annual temperature was 2.4 °C with summer maxima up to 32 °C and winter minima down to -28 °C. The soil is a haplic podzol with a 20-30 cm thick layer of raw humus on top of the mineral horizons (for further details see WIESER 2004b).

Environmental and gas exchange measurements

Irradiance was measured with n LI-190 PAR quantum sensor (Li-Cor, Inc., Lincoln, Nebraska 2 m above the canopy. Air temperatures and soil temperature were monitored with type T thermocouples at 8, 5.5, 3.5, 1.5 m above ground, and at 5 cm soil depth, respectively. Soil water potential in the top 10 cm soil layer was measured with an equitensiometer (Model EQ3, Ecomatic, Dachau-Munich, Germany).

CO$_2$ gas exchange of the last three flushes was measured continuously throughout the snow free period using two climate controlled cuvettes (Walz, Effeltrich, Germany). One cuvette was installed in the upper sun crown and another in the lower shade crown on the south and the north side of the tree, respectively. Shoots in the chambers were changed in weekly to biweekly intervals. Cuvettes were removed during the winter due to freezing of dew-point mirrors and cold traps.

Woody tissue and soil respiration was measured by means of a multiplexing open gas exchange system (WIESER & BAHN 2004, WIESER 2004b). A total of 10 unclimatised, clear "Perspex" chambers was fitted to branch, stem, and coarse roots for continuous monitoring of woody tissue CO_2 efflux. Additionally, cambium temperature was measured in and outside the chambers with 1 mm thin type T thermocouples. Relative to the tissue position outside the chambers mean maximum overheating of the tissue in the chambers reached 2.1 K during short periods of high irradiance but otherwise was negligible.

Six soil respiration chambers, made from PVC, were installed at tree locations: close and distant from the stem and in a gap within the canopy. Further details regarding construction and measurement instrumentation is reported by WIESER 2004b.

All pneumatic tubing was heated and insulated. Gas streams from all the cuvettes, chambers, and from the reference air, sampled 2 m above the top of the tree, were measured alternately by means of a solenoid-based, gas-switching system. CO_2 concentration of the air streams through the two foliage-cuvettes was measured with a Li-Cor 6262 gas analyzer (Li-Cor, Inc. Lincoln, Nebraska) operating in the differential mode and the corresponding flow rates were monitored with electronic mass flow-meters (Tylan, Eching, Germany), each cuvette being sampled for 3 minute intervalswith the first two min being ignored to ensure a total flushing of the ges analyser. CO_2 efflux from each of the ten woody tissue and three soil respiration chambers was measured every 15 minutes with a second Li-Cor 6262 gas analyzer operating in the absolute mode.

All 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.

Foliar CO_2 gas exchange data were based on needle dry weight, woody tissue CO_2 efflux rates were related to sapwood volume and soil CO_2 efflux to m^2 ground surface area.

Scaling to the annual budget

Components of C fluxes with respect to space (ecosystem) and time (entire year) were calculated from component-specific gas exchange measurements and estimated biomass (foliage, stem, branches, and coarse roots). Needle, stem, and branch biomass, was calculated based on allometric equations developed at the site (Fig. 1).
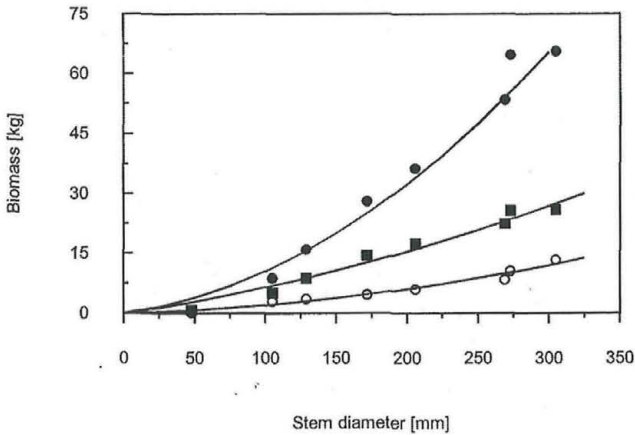

Fig. 1. Relationship between branch (closed circles), needle (closed squares), and stem (open circles) biomass of *Pinus cembra* with respect to stem diameter at breast height. Data are from a single tree and lines were fit by exponential regression: branches: $y=0.596*x^2+47.73*x$, needles: $y=0.127*x^2+51.77*x$; stem: $y=0.099*x^2+9.83*x$; For all tissues $r^2>0.95$.

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In order to avoid any destruction of the soil system, coarse root biomass was not determined and coarse root biomass was assumed to be 25% of the total biomass. This root mass ration was obtained from biomass allocation patterns derived from a wide range of *Pinus cembra* trees sampled within the timberline ecotone of the central Tyrolean (OSWALD 1963) and Swiss Alps (BERNOULLI & KÖRNER 1999) and was found to be conservative in trees older than 23 years.

The biomass of roots with a diameter < 5mm (in the following termed as small roots) of the top soil (0-30 cm soil depth) was based on 3 cores beneath each soil respiration chamber. Standing crops for each component are summarised in Table 1.

Table 1. Characteristics of the *Pinus cembra* stand. LAI = leaf area index

Parameter	
Stand density ha^{-1}	1038
Basal area (m^2 ha^{-1})	47.6
Projected LAI (m^2 m^{-2})	3.9
Foliage biomass (Mg ha^{-1})	17.9
Branch biomass (Mg ha^{-1})	42.5
Stem biomass (Mg ha^{-1})	7.6
Coarse root biomass (Mg ha^{-1})	22.7
Top soil small root biomass (Mg ha^{-1})	15.7

Foliar gas exchange data were combined with data measured previously during the cold season (WIESER 1997) in order to estimate the annual time course of daily total carbon gain, daily total night-time respiration and the annual carbon balance of the foliage. Stem sapwood volume (S_V, cm^3) was calculated by an allometric relationship with DBH according to: $S_V = 0.0047*\exp(2.64*DBH)$; $r^2 = 0.98$). Branch and coarse root sapwood volume was derived by dividing branch and coarse root biomass (Table 1) by specific weight (0.6 g cm^{-3}) because there was no heartwood in both, branches and coarse roots.

Small root respiration was separated from soil surface CO_2 efflux by using a regression between total soil respiration and small root density and found that soil-surface CO_2 efflux and small root biomass were significantly correlated by the exponential regression: $R_s = 9.06*\exp(0.22*M)$, where R_s is the total soil surface CO_2 efflux (g C y^{-1}) and M is the small root biomass. By using the y-intercept value to estimate mean hererotrophic respiration we calculated that small root respiration accounted for 65% of total annual soil surface CO_2 efflux. This ratio was used to appoint our total soil CO_2 efflux estimation between small root and heterotrophic respiration. However, we note that this equation does not consider seasonal changes in fine root biomass.

To compare the contribution of each respiration to ER we converted all fluxes into units of g C m^{-2} ground surface area d^{-1}. Other trees occasionally encountered in our plot were treated as *Pinus cembra* trees. However, their influence on the result is marginal because the contribution of *Picea abies* and *Larix decidua* to the total tree number at the site wads less than 9 and 8%, respectively. Furthermore at the study site, there were no significant differences in the annual carbon balance between evergreen and deciduous conifers (TRANQUILLINI & SCHÜTZ 1970).

Results and Discussion

The seasonal patterns of environmental parameters were representative for the climatic conditions in the timberline ecotone of the central Tyrolean Alps (Fig. 2). Daily mean air temperature varied between -14.4 °C on December 14, 2001 and +19.4 °C on June 19, 2002 (Fig. 2). Snow persisted from mid November until the end of April. The lowest daily mean soil temperature recorded during this study was -3.1 °C on January 15, 2002, and the highest daily mean soil temperature was

12.8 °C on June 23, 2002 (Fig. 2). Due to frequent precipitation during the snow free period soil water potential always remained above -0.06 MPa (Fig. 2), indicating that the forest was not subjected to soil drought.

C fluxes generally followed seasonal trends in temperature (Fig. 2) as has been observed in other boreal and temperate forest ecosystems (LAW & al. 1999, FALGE & al. 2002, HUXMAN & al. 2003, BOLSTAD & al. 2004, ZHA & al. 2004.). Daily NEP ranged from -3.05 during the winter (day 269) up to 9.86 (day 142) g C m^{-2} ground surface area day^{-1} during the growing season (Fig. 2). Continuous net CO_2 uptake began on day 110 and ended on day 297, resulting in a growing season of 186 days. GPP and ER had seasonal trends similar to that of NEP with the lowest values during the winter and the highest values during the growing season (Fig. 2). Maximal daily GPP was 14.9 g C m^{-2} (day 212) while daily ER ranged from 0.5 (day 314) to 11.05 g C m^{-2} day^{-1} (day 169).
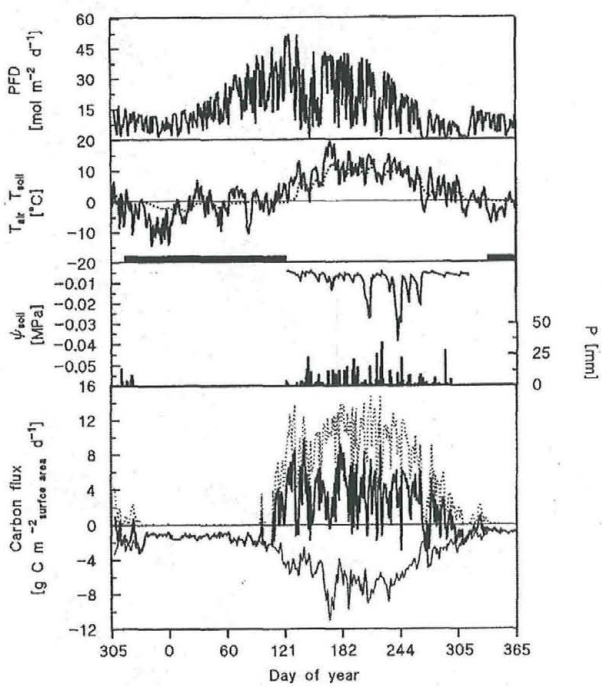

Fig. 2. Time course of daily sum of photon flux density (PFD), daily mean air (T_{air}, solid line) and soil temperature at 5 cm soil depth, (T_{soil}, dotted line) winter snow cover (solid area), soil water potential (Ψ_{soil}), daily sum of precipitation (P), as well as daily net ecosystem production (NEP; thick solid line), ecosystem respiration (ER; thin solid line), and gross primary production (GPP; (thin dotted line) in the *Pinus cembra* ecosystem under study between November 5, 2001 and December 31, 2002.

Cumulative GPP estimated during 2002 was 1610 g C $m^{-2} y^{-1}$ (Table 2); which is within the range of 831 to 1691 g C $m^{-2} y^{-1}$ estimated for other high altitude and high latitude coniferous forests (VALENTINI & al. 2000, FALGE & al. 2002, ZHA & al. 2004).

Annual ER was 1247 g C $m^{-2} y^{-1}$ and was mainly dominated by fluxes from above ground components (Table 2). The contribution of C efflux from the foliage, branches, and stems to total ER was 22, 68, and 4%, respectively (Table 2). The fraction of annual C efflux from coarse roots, small roots, and heterotrophic components to total ER was 4, 2, and 1 % respectively. These low C efflux rates from below ground components can be attributed to low root zone temperatures (WIESER & BAHN 2004) as well as a supra-optimal soil water availability, because soil water potentials exceeding -0.05 MPA were found to depress soil surface CO_2 efflux (WIESER 2004b).

Table 2. Annual gross primary production (GPP), ecosystem respiration (ER), component respiration and annual net ecosystem production (NEP) in 2002.

Parameter	g C m^{-2} surface area year^{-1}	%
GPP	1610	100.0
ER	1247	77.5
Annual foliage respiration	276	17.1
Annual branch respiration	846	52.5
Annual stem respiration	45	2.8
Annual coarse root respiration	50	3.1
Annual small root respiration	22	1.4
Annual heterotrophic respiration	11	0.7
NEP	363	22.5

Ecosystem carbon sequestration (= NEP) was 363 g C m^{-2} year^{-1}. Thus, the estimated annual NEP is comparable to values reported for other high elevation coniferous forest ecosystems (58 to 500 g C m^{-2} year^{-1}) in Snowy Mountains, Wyoming (ZELLER & NIKOLOV 2000) and in the Front Range, Colorado, USA (CAREY & al. 2001, MONSON & al. 2002). In a throughout study on NEP in forest ecosystems across a latitudinal transect in Europe VALENTINI & al. 2000 reported values ranging from 470 to 600 g C m^{-2} year^{-1} at latitudes lower than 51°N and values from -80 to 245 C m^{-2} year^{-1} at higher latitudes.

The ratio of NEP to GPP was 0.23 (=carbon use efficiency in terms of SAXE & al. 2001), and is within the mean range reported for temperate forests (0.28± 0.10) but below the range reported for boreal forests (0.17±0.12 by FALGE & al. 2002.

Throughout the growing season (day 110 -297) when net CO_2 uptake was not limited by cold temperatures the temperature response curve of GPP is relatively wide as net photosynthesis operates at more than 90% of its maximum at a temperature range between 5 and 20°C (WIESER 2004a) and air temperature explains 60% of the seasonal variation of GPP (Fig. 3). The remaining variation may

be attributed to changes in irradiance (data not shown) as there is evidence that the temperature optimum of C gain in *Pinus cembra* shifts towards lower values when irradiance is low (PISEK & WINKLER 1958, WIESER 1997). Thus, it seems that irradiance is a main determinant of the seasonal variation in net C gain once temperature had reached a level at which physiological processes are not limited. ER increased exponentially with temperature (Fig. 3; $r^2 = 0.84$). The annual Q_{10} was 2.45, while ER at 0 °C was 2.11 g C m^{-2} day^{-1}. Thus, the relationships observed for GPP and ER (Fig. 3) lead to the conclusion that, under current climatic conditions warm temperatures in mid-summer and their effects on ER are the key factor limiting NEP at the alpine timberline (c.f. also HUXMAN & al. 2003). Low temperatures by contrast are not necessarily a burden to the overall carbon sequestration of high elevation forest ecosytems.
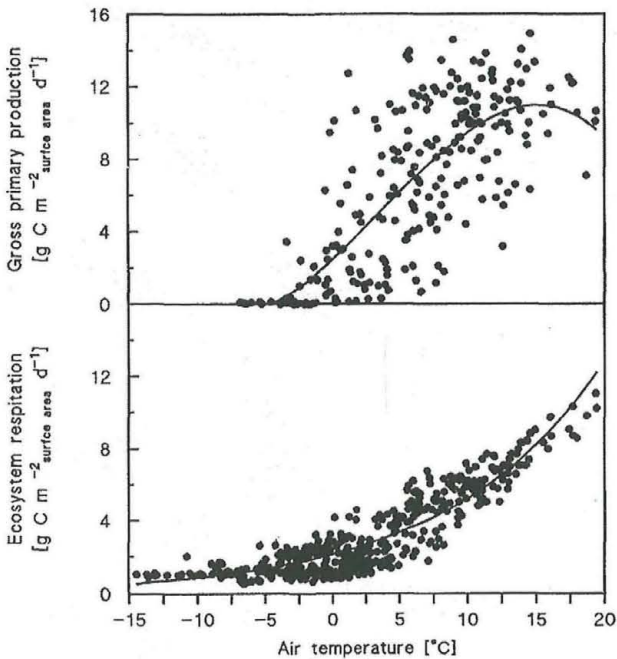

Fig. 3. Gross primary production during the growing season (GPP) and year round ecosystem respiration (ER) in relation to air temperature. Points were fit by regression analysis: GPP: $y=((-0.002*x+0.022)*x+0.68)*x+2.43$, $r^2= 0.60$; ER: $y=2.11*\exp(0.09*x)$, $r^2= 0.84$.

There is extensive evidence that the Earth's climate has warmed during the last century (JONES & al. 1988, WUEBBLES & al. 1999) and global climate models predict a further increase in mean air temperature of 1.4 to 5.8°C in the next century (IPCC 2001). On a regional scale this trend has been documented for the tim-

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berline ecotone on Mt. Patscherkofel for the last 40 years where the mean annual air temperature in the last decade was at an average 1.0 °C higher as compared to the 30 years before (Fig. 4) and appears to indicate that changes are greatest during winter and spring (WIESER 2004b). As a result, the duration of the snow free period was extended from 168 ± 12 days (years 1972-1985; HAVRANEK 1987) to 196 ± 23 days (years 1994-2002; WIESER 2004b). Growing season precipitation patterns by contrast, have not changed significantly during the last four decades.
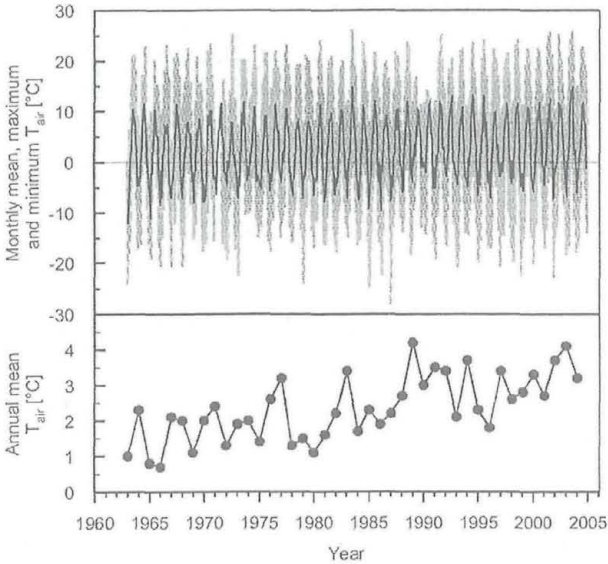

Fig. 4. Variation in monthly mean, maximum and minimum air temperature (top), and changes in annual mean air temperature (bottom) from January 1963 throughout December 2004 at the Klimahaus Research Station, 1950 m a.s.l. (Mt. Patscherkofel, Innsbruck, Austria.

Thus, carbon sequestration may change with predicted climate warming. Model estimations predict that a 3-4 °C increase in global temperature will reduce productivity (VEMAP MEMBERS 1995) because respiration is relatively more sensitive to temperature than photosynthesis (RYAN 1991, AMTHOR 1994). On the other hand respiratory rates may acclimate and adjust to new temperatures. There is ecidence that at a given temperature species from warmer environments have lower respiration rartes than those from colder environments (RYAN & al. 1996) and differences can be up to 50% as shown for *Picea abies* by PISEK & WINKLER 1958. Furthermore, on the long term respiratory fluxes may also be limited by substate supply (DEWAR & al. 1999) and hence must be linked with carbon upotake (SAXE & al. 2001).

Calculations based on the temperature responses shown in Figure 3 suggest that a 1.0°C increase in mean annual temperature will increase annual GPP and ER

of the *Pinus cembra* forest by about 15 and 10 %, respectively and thus leading to an increase in NEP of 5 % as compared to the present situation. Thus, carbon sequestration in high-elevation, subalpine forests may benefit from future warmer climatic conditions, as also suggested for boreal Scots pine forests in eastern Finland (ZHA & al. 2004). This idea is further supported by STRÖMGREN & LINDER 2002 who observed that six years of artificial soil warming caused a significant increase in the carbon sequestration of a boreal Norway spruce stand in Northern Sweden. However, further studies are needed to quantify predicted temperature-induced changes on various C fluxes in forest ecosystems within the timberline ecotone. One approach may be to conduct studies along altitudinal temperature gradients - from the closed forest to the upper limit of tree growth - where the ecosystem as a whole had time to adjust to long-term gradual changes in climate. Such studies can also be used to validate short-term artificial warming experiments (RUSTAD & al. 2001, STRÖMGEN & LINDER 2002).

Acknowledgement

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