Treeline trees in a CO_2-enriched world

The «Stillberg» Free Air CO_2 Enrichment (FACE) experiment was established in 2001 and has been successfully in operation for four growing seasons with the support of a dedicated team and the Swiss National Foundation. It is located on a mountain called Stillberg (Davos, GR) where a long-term research site of the Swiss Federal Institute for Snow and Avalanche Research exists.

The goal is to expose natural vegetation at the upper altitudinal treeline to an elevated atmospheric CO_2 concentration expected in the near future in order to investigate whether tree growth at treeline is carbon limited, and what changes are to be expected in the treeline ecotone with the continuing rise in atmospheric CO_2 concentration.

Major research activities are related to growth and carbon allocation in the two tree species *Larix decidua* and *Pinus uncinata*, growth of dwarf shrub species, potential advantages for hemi-parasitic plants such as *Melampyrum*, performance of herbivores feeding on CO_2-exposed forage plants, and to carbon and nutrient flux questions at the ecosystem level. These latter topics include a spectrum of soil related questions such as the effect of elevated CO_2 on dissolved organic carbon, soil respiration, and ectomycorrhizal development in treeline conifers.

Dischma valley, near Davos

Liquid CO_2 supply

Bird's eye view of the Stillberg site

CO_2-enrichment of treeline conifers

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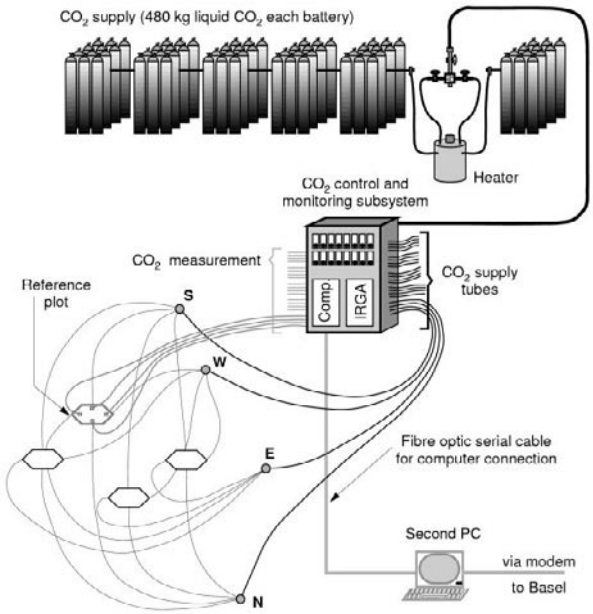
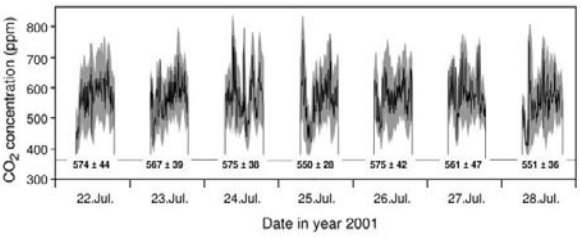
Technology of CO_2 enrichment

Twenty plots (each 1.1 m^2) are exposed to elevated CO_2 (target value of 550 ppm) using a FACE system with pure CO_2 release. Another 20 plots are used as controls at a current ambient CO_2 concentration (370 ppm). Liquid CO_2 is brought in by helicopter biweekly. CO_2 is then delivered to a control system in the field equipped with an infrared gas analyzer (IRGA) for CO_2 measurement, a control PC and an array of solenoid valves for CO_2 flow control. Four enriched plots are supplied with CO_2 according to actual CO_2 concentrations measured within a reference plot. The pure CO_2 release technology proved suitable for CO_2 enrichment of natural vegetation at our remote treeline site. Reliable CO_2 control was achieved comparable to previous FACE systems with relatively small fluctuations around the target CO_2 concentration. Seasonal averages of CO_2 concentrations (2001-2003; ± SD) were 566 ± 42, 582 ± 35 and 579 ± 52 ppm (data analysis courtesy of G. Grun).



Setup of the supply, control, monitoring and field enrichment of CO_2



Diurnal course of CO_2 concentrations over a representative week in July 2001. Mean of five reference plots (black line) ± standard deviation (grey area) are shown. Numbers indicate mean daytime CO_2 concentration.

Delivery of CO_2

Experimental plot

Tree growth

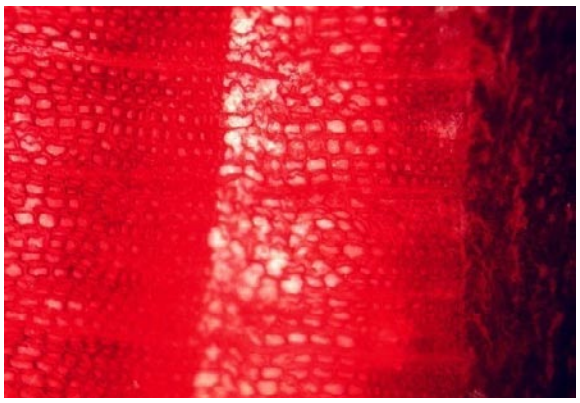
Historically, carbon limitation, through a shortage of photoassimilates has been argued to limit the growth of trees at the upper altitudinal treeline. We used CO_2 enrichment in combination with a defoliation treatment to test the effect of altered source-sink relationships on tree growth and leaf level responses of *Larix decidua* and *Pinus uncinata*. While *Larix* showed a stimulation in shoot growth and ring width over all four growing seasons when exposed to elevated CO_2 supporting carbon limitation, *Pinus* did not. However, when trees were defoliated in spring 2002, this response was reversed in the two species. We conclude that the expected changes in growth of these treeline conifers with improving carbon availability as atmospheric CO_2 continues to increase will thus depend on both the interplay between biotic and abiotic processes, and the species or tree functional type involved.

Shoot growth of *Larix decidua* and *Pinus uncinata*

Dwarf shrub growth

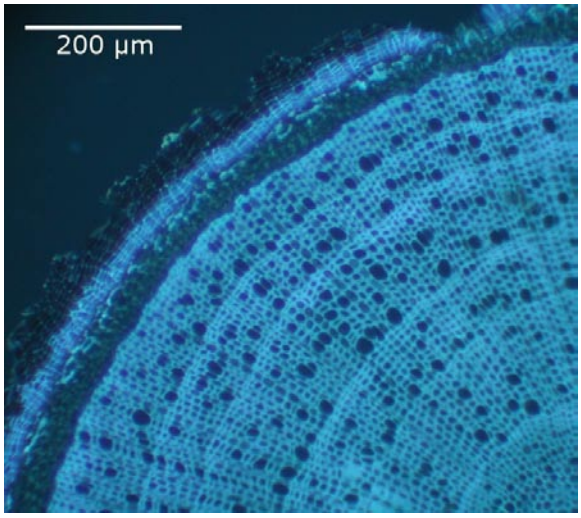
Different species of ericaceous dwarf shrubs occur at the site. CO_2 responses in shoot length growth, secondary stem growth and carbon allocation differed among species. Surprisingly, overall performance of dwarf shrubs in the vicinity of (deciduous) larch trees was generally better than in the vicinity of (evergreen) pine trees, which is probably due to higher soil nutrient concentrations caused by faster leaf turnover and decomposition of needle litter in larch trees. The results suggest that dwarf shrubs responded to elevated CO_2 in a species-specific way in the short term. However, it remains unclear whether these responses will persist in the long term and if the species-specificity will lead to changes in community composition.

Vaccinium myrtillus and *Vaccinium uliginosum*



Stained and magnified (200x) stem wood cells of *Larix*

Bird's eye view of the Stillberg site



Microtome slice of *Vaccinium myrtillus* stem

Dwarf shrub community

Plant-insect interactions

The chemical composition of plants growing in a CO_2 enriched atmosphere can differ from that of plants growing at ambient CO_2 concentrations. This change in leaf quality may have possible implications for higher trophic levels feeding on altered food plants. We tested this hypothesis by studying two herbivores in this alpine system.

The alpine grasshopper (*Miramella alpina*) is the most abundant grasshopper in the treeline ecotone at Stillberg and prefers Vaccinium species as feeding plants. Plant-species specific reductions in grasshopper growth and decreased reproductive output was observed in response to elevated CO_2, suggesting altered trophic interactions in a future CO_2-rich world. The larva of the grey larch bud moth (*Zeiraphera diniana*), a lepidopterous species (Tortricidae), is the most important leaf chewing insect herbivore of the larch-cembran pine forests in the central European Alps, causing large scale defoliations in these forests. We investigated the effects of elevated CO_2 and previous year defoliation on larch needle quality and larch bud moth performance. Larch bud moth larvae grew somewhat slower under elevated CO_2 compared to ambient CO_2 when trees remained undefoliated. If, however, trees were defoliated, this response was reversed, with a faster growth of larch bud moth on high CO_2-exposed trees than on control trees. Pupal weight was not affected by CO_2 or defoliation.

Above: *Zeiraphera diniana*
Left: *Miramella alpina*

Hemiparasite abundance

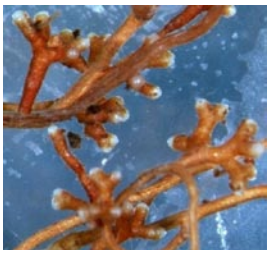
Populations of the annual hemiparasites *Melampyrum pratense* and *Melampyrum sylvaticum* were studied at treeline of the Swiss Alps after three years of CO_2 enrichment. Total abundance of *Melampyrum* doubled and plant height of the more abundant and more evenly distributed *M. pratense* increased by 20%, number of seeds per fruit by 21% and total dry mass per fruit by 27%, but individual seed size did not change. These results suggest that rising atmospheric CO_2 will stimulate reproductive output and increase abundance of *Melampyrum*, most likely as a consequence of improved host carbon uptake, which given the influence of hemiparasites on the N cycle may have important effects on community dynamics and ecosystem processes in the alpine treeline ecotone.

Melampyrum sylvaticum

Dwarf shrub community with *Melampyrum pratense*

Treeline conifer ectomycorrhizae

Effects of elevated CO_2 and defoliation stress on diversity of ectomycorrhizae of treeline conifers were studied by planting four month old sterile seedlings of *Larix decidua* and *Pinus uncinata* as probes under adult trees of the same two species for the 2003 growing season. According to ITS-RFLP typing, 20 ectomycorrhizal fungi were identified including 10 *Larix*-specific, 8 *Pinus*-specific and 2 unspecific morphotypes on conifer hosts. Increased atmospheric CO_2 concentration led to an increase in the number of morphotypes and diversity of morphotypes observed on *Pinus* seedlings but not on larch seedlings. Rhizomorph occurence increased on roots of both of the seedling species growing in plots exposed to elevated CO_2 with the exception of those growing under defoliated trees of the opposite host species. These results suggest that increases in atmospheric CO_2 concentrations may impact below-ground processes creating potential feedbacks at the ecosystem level.



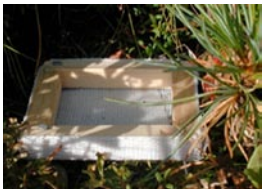
Three morphotypes of ectmycorrhizae

Below-ground soil responses

Plants are frequently observed to increase carbon allocation to below-ground sinks and to particularly accelerate fine-root turnover in response to elevated CO_2. While these strong below-ground responses have predominantly been observed in rapidly expanding systems, late successional plant communities have rarely been studied. We monitored fine root growth using ingrowth root cores, standing crop harvests and decomposition of roots using litter bags. Soil C dynamics were assessed by measuring fluxes of dissolved organic C, soil respiration and microbial biomass. Elevated CO_2 did not stimulate root growth of the treated vegetation nor did altered root decomposition occur. However, elevated CO_2 resulted in 20% more water extractable soil organic carbon and marginally higher soil respiration rates. Our data show that fine root growth may be much less stimulated by elevated CO_2 in late successional systems than in ecosystems with a rapidly expanding plant community biomass. The higher water extractable organic carbon measured at elevated CO_2, could have important implications for soil functioning by changing substrate availability for microorganisms or the potential for carbon loss from the system by leaching.

Soil water solutions for C analyses

Ingrowth root cores



Leaf litter trap

Carbon allocation in branch wood

Taking advantage of the d13C-depleted CO_2 used for the CO_2 enrichment, we assessed the relative contribution of stored and current carbon compounds to new shoot growth in larch and pine. Wood and needle material from trees exposed to both ambient and elevated CO_2 concentrations was collected and analysed for the 13C/12C-ratio. The deciduous larch was found to supply new shoot growth (structural woody part) by 46% from storage. Surprisingly, the evergreen pine which we expected to use current-year photosynthates for new wood growth, also considerably depended on storage (42%). In contrast, storage made only a very small contribution to needle growth (more decreased 13C/12C-ratio under elevated CO_2 conditions for needles than for wood). In wood, the 13C/12C-ratio of different wood fractions was determined. However, the allocation of new carbon to different fractions of the wood was similar. We conclude that storage plays an important role for new shoot growth in these treeline conifers. In particular, stored carbon compounds apparently are more relevant for current-year growth in the evergreen pine than has previously been thought.

Germinating cress plants

Wood sampling

Publications

Hättenschwiler S, Handa T, Egli L, Asshoff R, Ammann W, Körner C (2002) Atmospheric CO2 enrichment of alpine treeline conifers. New Phytologist 156: 363-375

von Felten, S (2003) Carbon allocation in new shoots of alpine treeline conifers in a CO2 enriched environment. Diploma thesis, Institute of Botany, University of Basel.

Zumbrunn T (2004) Alpine dwarf shrubs in a CO2 enriched world. Diploma thesis, Institute of Botany, University of Basel.

Serio D (2004) Mycorrhizal infection of seedlings at the Swiss treeline: effects of CO2 enrichment, defoliation and host species. Diploma thesis, Institute of Botany, University of Basel.

Asshoff R, Hättenschwiler S (2005) Growth and reproduction of the alpine grasshopper *Miramella alpina* feeding on CO2-enriched dwarf shrubs at treeline. Oecologia 142:191-201. DOI: 10.1007/s00442-004-1714-0

Handa IT, Körner C, Hättenschwiler S (2005) A test of the treeline carbon limitation hypothesis by in situ CO2 enrichment and defoliation. Ecology, in press.

Asshoff R, Hättenschwiler S (2005) Changes in needle quality and larch bud moth performance in response to CO2-enrichment and defoliation of treeline larches. Submitted.

Hättenschwiler S (2005) Global change driven increased hemiparasite abundance in an alpine treeline ecotone. Submitted.

von Felten S, Hättenschwiler S, Saurer M, Siegwolf R (2005) Carbon allocation in shoots of alpine treeline conifers in a CO2 enriched environment. Submitted.

Handa IT, Körner C, Hättenschwiler S (2005) Stem responses of treeline conifers to four years of in situ CO2 enrichment. In preparation.

Zumbrunn T, Hättenschwiler S (2005) Species specific growth responses of alpine dwarf shrubs after four years of CO2 enrichment. In preparation.

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