The «Stillberg» Free Air CO₂ 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 CO₂ 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 CO₂ 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 CO₂-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 CO₂ on dissolved organic carbon, soil respiration, and ectomycorrhizal development in tree line conifers.
**Technology of CO₂ enrichment**

Twenty plots (each 1.1 m²) are exposed to elevated CO₂ (target value of 550 ppm) using a FACE system with pure CO₂ release. Another 20 plots are used as controls at a current ambient CO₂ concentration (370 ppm). Liquid CO₂ is brought in by helicopter biweekly. CO₂ is then delivered to a control system in the field equipped with an infrared gas analyzer (IRGA) for CO₂ measurement, a control PC and an array of solenoid valves for CO₂ flow control. Four enriched plots are supplied with CO₂ according to actual CO₂ concentrations measured within a reference plot. The pure CO₂ release technology proved suitable for CO₂ enrichment of natural vegetation at our remote treeline site. Reliable CO₂ control was achieved comparable to previous FACE systems with relatively small fluctuations around the target CO₂ concentration. Seasonal averages of CO₂ concentrations (2001-2003; ± SD) were 566 ± 42, 582 ± 35 and 579 ± 52 ppm (data analysis courtesy of G. Grun).

![Delivery of CO₂](image1)

![Experimental plot](image2)

![Diurnal course of CO₂ concentrations](image3)
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.

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.
**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](image)

**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](image)
**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 occurrence 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.

**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.
Carbon allocation in branch wood

Taking advantage of the d13C-depleted CO2 used for the CO2 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 CO2 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 CO2 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.

Publications


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