Plant responses to long-term in situ CO2 enrichment and soil warming at treeline in the Swiss Alps

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In situ studies lasting several years are essential for predicting how plant growth and ecosystem function will change under rising levels of atmospheric CO2 and the associated changes in climate. High-latitude and high-elevation ecosystems are predicted to be particularly sensitive to environmental change, but relatively few manipulation experiments have been conducted in these regions. This doctoral thesis describes responses of two co-occurring tree species, Larix decidua and Pinus uncinata, and understorey dwarf shrub heath vegetation to 9 years of CO2 enrichment (+200 ppm; 2001-2009) and 3 years of soil warming (+4 K; 2007-ongoing) at treeline in the Swiss Alps (Stillberg, Davos).

We tested if elevated CO2 stimulates tree growth in an environment where there is strong evidence that low temperature limits growth despite an adequate carbon supply. For this investigation, we pooled across soil warming treatments in order to focus on long-term responses to elevated CO2. Larix ring width was stimulated by CO2 enrichment throughout the treatment period, with a significant stimulation in years 3-7, while Pinus ring width showed no CO2 effect. After 9 years of treatment, leaf canopy cover, stem basal area, and total new shoot production were greater in Larix trees growing under elevated CO2, whereas Pinus showed no cumulative growth response. Larix ring width was stimulated more by elevated CO2 in years with relatively high spring temperatures and an early snowmelt date, suggesting that temperatures were less limiting in these years and greater benefit was gained from extra carbon assimilated under elevated CO2. The CO2 effect size was also larger after relatively high temperatures and high solar radiation in the preceding growing season, perhaps reflecting gains due to larger carbon reserves. Contrasting responsiveness of these two species suggests that under future CO2 concentrations, especially in combination with warmer and sunnier conditions, Larix will have a competitive advantage over less responsive species such as Pinus.

Dwarf shrubs are a major component of alpine plant communities, and changes in the growth, abundance and distribution of these species are likely to have important ecological consequences. We studied growth responses of three dominant dwarf shrub species, Vaccinium myrtillus, Vaccinium gaultherioides and Empetrum hermaphroditum, to CO2 enrichment and soil warming and how the treatments influenced understorey community composition. V. myrtillus growth was stimulated by elevated CO2, with no

decline over time in the annual shoot growth response, and to an even greater extent by soil warming. V. gaultherioides growth showed a slight positive effect of elevated CO_2, though only in experimental plots with Pinus, and no response to warming. E. hermaphroditum growth was not influenced by either treatment. Vascular plant species richness decreased in elevated CO_2 plots with Larix but not with Pinus, while the number of moss and lichen species decreased under soil warming. Overall, species-specific dwarf shrub growth responses indicate potential shifts in plant community composition at the alpine treeline.

The frequency of freezing events during the growing season and the vulnerability to freezing of plants in temperate high-elevation environments could increase in the future. We conducted an experimental freezing study to determine effects of CO_2 enrichment and soil warming on the early growing season freezing resistance of 10 plant species. Long-term exposure to elevated CO_2 led to reduced freezing resistance in 5 species but did not influence phenology, implying that physiological changes caused by CO_2 enrichment were responsible for the effect. Soil warming showed little to no influence on the freezing resistance or phenology of the sampled species. Our results suggest that leaf tissue damage caused by episodic early season freezing events will increase in frequency for some species in the coming decades. The resulting shifts in relative freezing resistance among co-occurring species could alter competitive interactions.

In an investigation of how the first season of soil warming influenced soil processes and ecosystem carbon balance, we found that soil respiration rates increased immediately with increased temperature while DOC leaching showed a delayed and much smaller response. Tracing of ^{13}C-depleted CO_2 added for 7 years showed that the accelerated CO_2 effluxes from warmed soils were not driven by increased mineralization of recent plant litter and root respiration but by mineralization from older soil organic matter. Soil carbon losses clearly exceeded the estimated carbon accumulation by plants, which showed little response to one growing season of soil warming. These findings suggest that soil warming, representative of warmer and drier years, can lead to short-term carbon losses from alpine treeline ecosystems.

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