

## Questions and answers to KÖRNER et al. *Science* 309:1360–1362 (2005)

A number of recurring questions came up which refer to this article, and often resulted from the shortness of the text that could not cover all these aspects. Most of the questions concerned the tree growth response, although the study had offered many other aspects of tree responses. Here we try to answer some of the more frequent questions:

### (1) Is 530 ppm CO<sub>2</sub> enough to see a signal?

The CO<sub>2</sub> effect on any plant function, including growth, is not linear, but follows a saturation function. The closer one approaches the saturation level, the smaller the relative gain. The lower the range the more effective any increment becomes. This even led some researchers (RF SAGE, 1995, *Global Change Biology* 1:93–106) to assume a critical role of the 200–270 ppm CO<sub>2</sub> transition for the onset of crop cultivation and the first urban cultures during the Pleistocene. All outdoor CO<sub>2</sub> experiments are constrained today by the already very high current ambient CO<sub>2</sub> concentrations of 377 ppm as a control. It is very likely that much of the CO<sub>2</sub> stimulation of plants, if there was any, happened in the recent past. Never the less, society will have added soon another 150 ppm (estimates range from 50–80 years from now), and hopes have been tied to this further increase that it might in part be mitigated by trees sucking up more C. So the range of concentrations considered here, is very much in the range of interest. According to a suite of indoor studies with more than one CO<sub>2</sub> concentration, it emerged independently in many laboratories (I recall several of Boyd Strain's works), that 550 ppm is a concentration at which responses reach a maximum, and then decline relative to this maximum, but still represent a gain compared to controls. We do not really understand this phenomenon, but it may have to do with increased nutrient shortage, induced by carbon compound exudation and microbial competition (e.g. S. DIAZ et al. *Nature* 364:616–617, 1993). One of the few studies which used a 4-step CO<sub>2</sub> enrichment starting from pre-industrial levels clearly supported this optimum range (Granados and Körner, *Global Change Biology* 8:1109–1117, 2002). Also *in situ*, tree seedlings were not found to get further stimulated when CO<sub>2</sub> concentrations were increased beyond 560 ppm (HÄTTENSCHWILER and KÖRNER, *Global Change Biology* 6:213–226, 2000). With our actual 530 ppm concentration, we thus optimize the cost-effect ratio, given the enormous gas bills. We missed the desired optimum by 20 ppm, but still operate at a ca. 150 ppm increase, in a range where plants are known to be very responsive.

### (2) Did the gas really reach the trees?

This is a very valid question and we spent nearly half of our personnel costs and a lot of technology on assessing this. First we have a spatially very broad high speed sampling system. Unlike conventional FACE systems with pre-mixed gas and blowers, this is critically important in a pure CO<sub>2</sub> release system in a rough canopy, 35 m above the ground. We have two independent gas sampling systems. One which samples instantaneously on a second basis 69 positions in the canopy (23 triplets of sampling lines in the canopy) and delivers this mixed signal to the control computer. A second, which samples 25 discrete canopy positions in a 2 minute switch cycle throughout the whole season to produce a spatially discrete picture of the gas concentration in the canopy. Both data sets are analysed by high resolution frequency distribution as described by PEPIN and KÖRNER (2002, *Oecologia* 133:1–9).

In addition we run two independent stable carbon isotope assessments. Here we take advantage of the different <sup>13</sup>C signature in ambient air CO<sub>2</sub> and in the fossil fuel derived CO<sub>2</sub> used for CO<sub>2</sub> enrichment. The isotope mixing ratio tells us how much additional CO<sub>2</sub> a leaf has seen. One test system uses so-called isometers, potted C4 grasses hung up in the canopy and watered from the gondola. They represent a multipoint biological integrator of isotope signals. The other one are the trees themselves, where we follow the isotope signal from leaf to root, as explained in the paper.

Thirdly, we conducted a series of short term measurement campaigns. One used a 3-D multipoint sampling with Dräger tubes and PET-flasks, which fully supported the long term data. Another one addressed the question of the influence of variable versus constant CO<sub>2</sub> enrichment (S. PEPIN unpublished). Because of wind any free CO<sub>2</sub> enrichment experiment will create such variation, and web-FACE possibly more so than conventional, blower driven FACE. This is the price to be paid for the greater realism of any FACE type CO<sub>2</sub> enrichment. We simulated various sharply oscillating CO<sub>2</sub> scenarios around selected branches (branch bags) and compared stomatal conductance with control branches receiving a constant mean CO<sub>2</sub> concentration, and we found no difference. Whether the photosynthetic machinery itself is influenced is uncertain, but it seems, on its path through the mesophyll and cell walls the most rapid oscillations are likely to be smoothed out. The limited evidence from the literature is still controversial. While HENDRY et al. (1997, 1999 see HOLTUM paper) find no

effect, HOLTUM and WINTER (*Planta* 218:152–158, 2003), simulating 20 s cycles, found reduced CO<sub>2</sub> stimulation of C uptake.

All in all, the gas certainly reaches the trees and ensures that CO<sub>2</sub> supply is significantly enhanced as desired.

### (3) Are the results of this CO<sub>2</sub> experiment in contradiction to others?

Not really, if one does not compare apples with pears. There is consensus in the scientific community that the degree to which a CO<sub>2</sub>-driven stimulation of photosynthesis translates into a growth stimulation depends on plant growth conditions and on duration. If one removes all other limitations to plant growth (e.g. nutrients) as may be applicable in horticulture, CO<sub>2</sub> enrichment can stimulate growth substantially. If these constraints, which exist to some degree in most terrestrial systems, come into play, the growth response will be diminished, depending on these constraints. Even lay persons understand that organisms are not made of pure carbon and that all the other chemical elements needed for life are not available in infinite quantities. So the question only is, when they become limiting and where. A suite of studies clearly documented a time dependency of CO<sub>2</sub>-driven growth responses in plants grown in soil, simply because at the start of the test, these resources did not constrain growth or, more likely, plants used their capability to either better explore these resources (e.g. more and deeper roots, better carbon supply to mycorrhizal fungi) and/or diluted their concentration in the plant body. Obviously, this cannot go on for ever, hence the classical initial response to a step increase of CO<sub>2</sub> concentration. This problem becomes more significant in long lived organisms which depend on annual recycling of nutrients through litter decomposition. If one groups available data in the literature by such criteria, two things become obvious:

(a) By far the greatest number of experiments were done with plants either grown under artificially enhance nutrient supply, or with plants which were young and had ample space to fill (a surrogate for resource supply), or the tests were very short. Only perhaps 10–15 of all studies out of many hundreds were conducted with test systems which depended on their own, local nutrient cycle and in which soils were not disturbed in the recent past (another surrogate for nutrient provision). The latter, «self-supporting» systems, are still those systems which feed >90% the world's biomass pool. Because the abundance of studies of the two types is extremely asymmetric, any pooling of data (e.g. in a meta-analysis), will always lead to results which reflect the relative abundance of the fast growing, simple systems. Obviously this is not doing any justice to reality. So meta-analysis of CO<sub>2</sub> effects makes no sense at all,

unless data are stratified by the major co-variables of CO<sub>2</sub> stimulation (KÖRNER, *Plant Cell Environ* 18:1101–1110, 1995; *New Phytologist* 159:537–538, 2003).

(b) If one now takes a closer look at the results of test systems in the „self-supporting nutrient“ category, the findings of the Basel experiment do not stand in isolation at all, although several of these other systems are unfertilized perennial grassland systems. However, time permitting, even some fertilized systems come down. So we do need to treat any test system, which is «open» in terms of nutrients, as for instance the famous salt marsh CO<sub>2</sub> experiment near Washington, as a separate category, more similar to agricultural systems. Of the two oldest and largest CO<sub>2</sub> enrichment experiments with trees, the one at Duke University (loblolly pine plantation) and the other one at Oak Ridge National Laboratory (sweet gum plantation), the first one shows a ca. 20% stimulation of stem growth, the second one shows none, as in the case of the trees studied here. Among other studies with trees, which used natural or mature stands (a very young poplar plantation on an alluvial plain would not fall in this category), I refer to the scrub oak works by B. HUNGATE et al (pers. com.) in Florida, which showed a clear initial re-growth response to CO<sub>2</sub> after fire (high nutrient availability, little competition), which disappeared as time progressed. Similarly, HÄTTENSCHWILER et al. found such a decline in signal size with time in oak trees in two independent CO<sub>2</sub> spring areas in Italy (*Global Change Biology* 3:436–471, 1997). If we go for undisturbed (in the sense of tilling, planting, fertilizing) grassland, the oldest data come from the long-grass prairie in Kansas (OWENSBY et al.), and this system provided early evidence for what became clear in a recent synthesis by MORGAN et al. (*Oecologia* 140:11–25, 2004), that the growth/biomass responses seen in grassland, could almost completely be explained by water savings in the soil, rather than photosynthetic responses per se, thus making results dependent on whether the atmosphere would feed back on these systems by reduced air humidity (greater evaporative forcing) or whether the climate will stay as it is or change in the future. The only multifactorial test of water x nutrient x CO<sub>2</sub> x warming interactions is conducted in Californian annual grassland, and so far shows negative CO<sub>2</sub> effects on growth, when combined with other treatments (SHAW et al., *Science* 298:1987–1990, 2002). A highly replicated 4-season study of completely undisturbed alpine turf in the Alps revealed a zero CO<sub>2</sub> effect (KÖRNER et al., *Acta Oecologica* 18:165–175, 1997), despite the «thin air», and thus reduced partial pressure of CO<sub>2</sub> at 2500 m elevation.

In summary the results obtained at the Swiss forest canopy crane are in line with a series of other studies conducted in systems which operate at a natural local nutrient cycle, but 4 years may not be enough, as we

clearly say, to arrive at a conclusive answer. These results must not uncritically be compared with responses seen in isolated, close to hydroponic orange trees, young sapling plantations or potted tree seedlings.

**(4) Is the number of trees studied enough to arrive at a conclusive answer?**

There are never enough. But this experiment with 30–35 m tall, close to 100 year old trees is obviously constrained by the fact, that the 12 tree canopies we had in the ca. 500 m<sup>2</sup> CO<sub>2</sub>-enriched zone plus the 29 control trees, growing in ambient air under the crane, show different individual growth, even before we started to elevate CO<sub>2</sub> concentrations. This natural variation would disguise any potential CO<sub>2</sub> signal. Therefore, we do NOT compare tree growth per se. Instead, we make use of the unique opportunity in working with tall trees that each individual has its own life history engraved in its tree-rings. We thus used the growth of the 5 years before the treatment of each individual to standardize its growth during the treatment. Although we explain this key element of our analysis in detail, some readers seem to have overlooked this. Our signal thus becomes largely independent of the individual's specific vigor, which is the basis of our statistical analysis. It turned out that 2 tree individuals of which there was only one per species in the CO<sub>2</sub> enriched zone did not grow measurably, although their crowns were green and used in leaf studies (one cherry and one maple), which reduced our sample to 10 elevated CO<sub>2</sub> trees, all of which were healthy and showed vigorous growth, the same applies to the 29 control trees. Pre-treatment data play a key role to account for a priory variation also in all other analysis. We have not seen such rigorous account for a priory variation in other experiments. One needs to see growth data prior to treatment to see whether a treatment really added an effect.

With the given sample size, we can and do not draw any conclusions for a specific species' long term response. Our sample are 10+29 trees, irrespective of taxa, all standardized for pre-treatment growth. Given the contrasting results of the loblolly pine and the sweet gum study, such species diversity in our sample makes conclusions more robust and less likely to reflect the peculiar response of any individual species. So, for people interested in tree responses in general, such a data set maybe more useful than one of a particular species. However, we do acknowledge that a larger experiment would be highly desirable, one of the reasons, why OSMOND and KÖRNER have successfully suggested to the International Botanical Congress in Vienna to urge an international effort towards such tests in the congress resolution <http://www.IBC2005.ac.at/>.

**(5) Are 4 years enough?**

No, that's what we clearly say. But 4 years is a good time to draw a first picture. All other experiments with taller trees have also rightfully waited 2–4 years before drawing first conclusions on growth responses. This needs also patient funders! If there were annual responses, smaller to be detectable on an annual basis, these should still accumulate into a signal, that might become measurable after 4 years. This is the benefit of working with trees compared to grassland. Since the difference across trees was numerically zero after 4 years (not just «not statistically significant»), we felt these results are not a strong support of a CO<sub>2</sub> stimulation hypothesis of tree growth. Given the weight this hypothesis has gained in the CO<sub>2</sub> debate based on models using first principles gas exchange equations (a far way from a tree growth response) or responses of much smaller test systems, very different from a forest, we felt it was appropriate to add our results to the two other existing data sets for two plantation forests (the Duke and the Oak Ridge test). While we definitively need more years, it seems still appropriate not to hide what we see, six years after we started working on this project.

Readers will have noticed, that we were very careful with our wording. We did not talk about productivity or carbon sequestration, we simply reported growth data for tall trees and litter production together with a suite of other data. It does not come at a surprise that journalists confuse growth with carbon sequestration, when even scientists do (see 6).

**(6) So forests don't matter for carbon storage?**

Sure they do. They matter more than any other part of the biomass components of the biosphere. They store most of the biomass carbon. Hence if we want to store more carbon in wood, we need more forests, or denser forests, or heavier forests. But CO<sub>2</sub> experiments have little to contribute to this debate, because we do not know how long trees are going to live under elevated CO<sub>2</sub>. Foresters do not wait for a certain age of trees, they harvest when trees reach a certain size. Should trees reach that size earlier, they will be cut earlier, removing any long term effect of growth stimulation on carbon storage at landscape level, but yields would go up. The only other pathway of extra carbon uptake to increase C storage is via soil carbon pools. Our paper does not contribute to this interesting debate, and given the signal to noise ratio the available data in this field are far from being conclusive. On a global scale we miss 30 g C per year per 20.000 g humus-C per m<sup>2</sup>, if we account for the 100 Mio km<sup>2</sup> vegetated terrestrial area. A very small signal after the globe has passed through the most effective range of atmospheric CO<sub>2</sub> enrichment from 270 to 377 ppm. At least not a signal easy to detect at plot scale.

Even if such C storage would occur, it would be good to remember that, unfortunately, it's not diamonds or coal which is stored (pure C), but any C added to the soil ties up with it a suite of other elements (not just N) and thus, removes these elements from plant availability. Not so good for growth.

This debate suffers from a rather fundamental misunderstanding, namely the confusion of fluxes (or rates) with pools of carbon. This is as if one would confuse cash flow with capital. We know the consequence. A growth rate does not permit any conclusion with respect to capital (C pools) unless one knows the residence time of the accreted biomass and its landscape wide distribution. Carbon stocking estimates need to include return times and disturbances (KÖRNER, *Science* 300:1242–1243, 2003) to become relevant. If there occurred some initial «buying time» due to ongoing CO<sub>2</sub> enrichment, we are in the middle of it, and it is unlikely to go on for ever. There rather is evidence for earlier tree maturation (LADÉAU and CLARK, *Science* 292:95–98, 2001) and tropical forests, the largest biomass-C pool on earth, may become more dynamic and in fact, may store less carbon in a CO<sub>2</sub>-rich future if lianas get «crazy» (KÖRNER, *Phil Trans R Soc Lond Ser B-Biol Sci* 359:493–498, 2004).

Should elevated CO<sub>2</sub> cause forests to store more carbon, one of the major pre-requisites (not the only) would be enhanced tree growth, at least in young to middle age forests. Since we do not find this after four years, we can only say that this pre-requisite's signal appears doubtful, but there may be other pathways, such as rhizosphere/soil processes which may have such a desired effect. We have presented no data on this, but it will remain a key research field at our site. So if any newspaper claims that «Swiss scientists found no evidence of carbon sequestration in forests», this is not what we ever said. How could we? The problem really is that our own scientific community is confusing these things....

### (7) What else are you studying?

A main emphasis are tree water relations. We have now several years time series of stomatal responses, sap flux and soil moisture data, which we will use in a synthesis work soon. For earlier releases see CECH et al. (*Oecologia* 137:258–268, 2003).

Stable carbon isotope work is a second core field. We aim at a complete picture of carbon flows in a forest, given the experiment offers this unique possibility. This is rather contributing to basic science, but will help interpreting CO<sub>2</sub> enrichment data. See: STEINMANN et al., *Oecologia* 141:489–501, 2004.

We have several projects on plant-animal interactions, facilitated by crown access by the canopy crane. Note that we reported differential leaf nitrogen and carbohy-

drate responses in canopy leaves of different species in our *Science* report. See for instance: HÄTTENSCHWILER and SCHAFELLNER *Global Change Biology* 10:1899–1908, 2004

### (8) For how long are you going to run the experiment?

We have currently completed 5 years and hope to receive funding for another 3 years starting in January 2006, which brings us to 8 years by the end of 2008. Depending on the year-to-year noise of data, we may then append 1–2 years, but not more, given the enormous costs of gas which reduce our funding for research personnel. Given that this experiment is not a «forest» experiment but is based on tree responses, this may be enough to arrive at a coherent picture. A forest experiment with trees of this size would only be feasible at several times the current costs, requiring three instead of one crane site, at the least.

### (9) At what cost are you running this experiment?

Not counting the academic and technical staff at the University (in total, 1.5 person-year of mixed status) the project currently runs at ca. 240 kEuro per year. The initial cost to start the project (crane, site logistics, cabins, CO<sub>2</sub> control) was about 300 kEuro.

#### Current sources:

- Swiss National Science Foundation (operating costs, no personnel)
- Swiss National Science Foundation's NCCR-climate program (water project, 1 PhD, 0.5 technician)
- Paul Scherrer Institute, Villigen (isotope works, 1 PhD).

#### Previous funding:

- BUWAL, the Swiss Agency for the Environment, Forests and Landscape (crane)
- BBW, the Swiss Federal Office for Education and Science in cooperation with the European COST program (1 PhD).
- Plus a number of smaller partnerships with crane users.

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