
Chapter 2

CO₂ Fertilization: When, Where, How Much?

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2.1 Carbon a Limiting Plant Resource?

Among the certain facets of global change, the steady CO₂ enrichment of the atmosphere affects plants directly. CO₂ is a substrate for photosynthesis, and for most (C₃) plant species CO₂ concentrations will remain below saturation levels of photosynthesis even at twice-current concentrations. Thus, the photosynthetic CO₂ response curve (a saturation function with a near-linear initial part and a plateau reached at close to 1 000 ppm) became the corner stone of modeling the biological consequences of rising of CO₂, because it was assumed to represent the degree of CO₂-fertilization in plants. In fact, models built around this response function forecast an approximately 290 Gt carbon sequestration into the terrestrial biosphere (biomass and soils) within the 21st century (e.g., Cao and Woodward 1998; IPCC 2001), raising hopes for a significant biotic mitigation of atmospheric CO₂ enrichment, which currently measures 3–4 Gt C yr⁻¹.

Thirty years of research, the most active part in the GCTE decade (1993–2003), have produced an estimated more than 4 000 publications (Körner 2000) in essence testing this or related hypotheses. It turned out that the rate of CO₂ uptake per unit leaf area is a rather unreliable predictor of plant growth and the cascade of follow up ecosystem processes. This limits predictions of future plant growth and crop production and it also restricts the credibility of estimates of the amounts of carbon that could be sequestered to the biosphere as a result of ‘CO₂-fertilization’.

Still not fully resolved, the discrepancy between photosynthetic stimulation by elevated CO₂, which is almost always observed, and actual plant growth responses, which vary considerably, became a central problem in predicting both the biosphere’s future in a CO₂-rich world and the potential of biological mitigation of atmospheric CO₂ enrichment. A related quandary has been the observed stimulation of growth in the less common but important C₄ class of plants through elevating CO₂ above present ambient levels (Wand et al. 1999; Ghannoum et al. 2000), since C₄ photosynthesis was thought to be saturated at present atmospheric CO₂ concentrations (Bazzaz

1990; Bowes 1993). A weak quantitative linkage between photosynthesis and growth (or yield) has long been known among crop breeders (Evans and Dunstone 1970; Saugier 1983; Wardlaw 1990), and there are many reasons for the mismatch between the CO₂-stimulation of photosynthesis and the actual biomass responses, but the most important ones are:

(1) The photosynthetic uptake of CO₂ depends on the total photosynthetically active surface of a plant and its integrated CO₂ flux activity over time (not easily quantified in discontinuous leaf-level gas exchange measurements) relative to its respiratory losses by heterotrophic tissue, (2) CO₂ release by respiration, which likewise depends not only on tissue specific rates but on the contribution of various, differentially active tissues to total plant biomass, and (3) the unknown export of assimilated carbon through roots, either directly to the rhizosphere microbe community or to mycorrhizal fungi.

With these and some other minor components of the internal carbon housekeeping, plants co-control their carbon investment in addition to their control over photosynthesis. The relationship between carbon uptake (source activity) and carbon investment (sink activity) drives the net outcome in terms of growth and biomass production.

It is obvious that these carbon investments also depend on resources other than CO₂, in particular mineral nutrients. A common effect of short-term plant exposure to elevated CO₂ is a reduced consumption of nutrients, but also water, per unit of biomass produced (Drake et al. 1997) or a constant consumption at greater biomass per unit land area (Niklaus and Körner 2004). In cases where total nutrient uptake is increased under elevated CO₂ (Finzi et al. 2002) this will deplete soil resources in the long run. In cases where tissue nutrient concentrations are depleted, this will induce cascades of negative ecosystem level feedbacks, which eventually may also cause initial rates of carbon gain to diminish. In many cases, it became questionable whether carbon is a limiting resource at the whole plant or ecosystem level (Körner 2003a). It is worth recalling that all taxa of today’s biosphere grew and reproduced successfully with only 180–190 ppm, half the current CO₂

concentration, 18 000 years before present (peak of last glaciation). Based on this reference period, current biota operate already in a double CO₂ atmosphere. In addition, the observed reduction of water consumption per unit land area is likely to induce climatic feedbacks (through a drier atmosphere), not yet accounted for in experiments. Furthermore, any CO₂ enrichment effect on plants will depend on their developmental stage, with younger plants more responsive than older ones (Loehle 1995). Most of the CO₂-enrichment responses for woody species available to date are – for very practical reasons – for young, rapidly expanding life stages, during which carbon is more likely a limiting resource.

All together these interdependencies are making predictions of the biosphere's overall response to elevated CO₂ far more difficult than was thought initially in view of the straightforward photosynthetic CO₂ response of leaves. The experimental evidence exemplified here, points at the need to reconsider the largely source activity dominated model parameterisation and to account for the constraints to carbon sink activity. Using current atmospheric carbon relations, Schimel et al. (2001) find the biosphere roughly in balance, i.e., deforestation being balanced by new C-fixation, part of which is due to forest expansion, hence leaving a much smaller leeway for CO₂-driven C-sequestration compared to what was anticipated during the 1980s.

In contrast to theoretical models, experiments are limited in space and time, and manipulations may disrupt ecosystem processes and thus, can create artifacts, though directions of responses are commonly still identified correctly in such situations (Norby et al. 1999). A major limitation, however, is that more than 80% of the Earth's life biomass is stored in wood, but trees are too big to be studied in conventional test systems, and it is nearly impossible to put a mature forest into an enclosure. Free air CO₂ enrichment (FACE) at such scales entails exorbitant costs, so that tests remained restricted to a few places and mostly fairly young trees. FACE refers to a CO₂-release system that does not need any enclosures, but freely releases (controlled by a computer in connection with an infrared gas analyser) CO₂ over test plots. The situation is far better for grassland and agricultural crops, where the low stature vegetation permits smaller CO₂-enrichment plots and where enclosures create fewer artifacts.

In this summary we will highlight what we think were major achievements during the last decade and we will restrict our considerations to the most realistic field tests, largely but not exclusively, using free air CO₂ enrichment *in situ*. Given the urgent need for forest data, these will receive particular attention. We will not re-review this vast field, but will try to illustrate the major lines of evidence and future needs in this arena of global change research.

2.2 Long-Term Biomass Responses and Carbon Pools

Whether a measured biomass gain under a step increase of CO₂ and otherwise unchanged life conditions reflects a change which might be seen in the real world, depends on three factors: time, nutrients and water. In addition, global change factors in the real, future world like temperature change (apart from effects on water, see Norby et al. 2007, Chap. 3 of this volume), light (change in cloudiness), and biotic interactions, will co-determine CO₂ effects. There have been few attempts at deciphering such interactions under realistic test conditions (see e.g., Rawson 1992; Shaw et al. 2002; Vonder et al. 2004; Wan et al. 2004) and the answers so far are inconclusive, with no clear interactive effect (Pendall et al. 2004). The general impact of a warming climate on the carbon balance of ecosystems will be dealt with elsewhere in this volume (Norby et al. 2007, Chap. 3 of this volume). We will, however, refer to the significance of interactions between CO₂ and light for tree seedlings and lianas in shaded habitats.

2.2.1 Time Matters

Plants with determinate growth (annuals, many crops) may grow faster initially at elevated CO₂, but end up with similar biomass accumulation per individual a couple of days or weeks earlier than controls, except under very fertile conditions. This was so for most of the 25 species of semi-desert winter annuals from the Negev desert of Israel, grown for their full life cycle in elevated CO₂, with only one species, namely one of the five legumes (the most 'mesic' one), taking great advantage of CO₂ enrichment, causing the whole sward to end up with more biomass (Grünzweig and Körner 2001, Fig. 1). In seedlings or saplings of woody species, such initial responses (when space and nutrients are ample and plants are very leafy) will cause future growth to capitalize on size differences induced by CO₂ very early in their life (analogous to compound interest in economics), which has nothing to do with ongoing CO₂ stimulation. Such initial responses simply shift the growth curve in time (Norby et al. 1995; Loehle 1995; Körner 2000; Spinnler et al. 2002) and cause the date of harvest to determine the difference in biomass gain.

Among the many other time dependent drivers of plant and ecosystem CO₂ responses, changes in community composition are important, and soil responses are particularly critical, given the size and slow turnover of soil C pools. Most of the humus carbon stored in soil is of very old age (often >1 000 years) and only a small fraction (commonly <1% in steady state systems) participates in year to year C-turnover. Mass based assessments of soil carbon are thus near to impossible. On the other hand, carbon tracer experiments with true control (also the ambient CO₂ system being labeled at the same rate)

are restricted to small scale, highly disturbed test systems (e.g., Leavitt et al. 2001; Niklaus et al. 2001). So, experiments provide rather limited access to the long-term fate of C in soils, but may point at some likely trends.

2.2.2 Nutrients and Water Determine Biomass Responses at Elevated CO₂

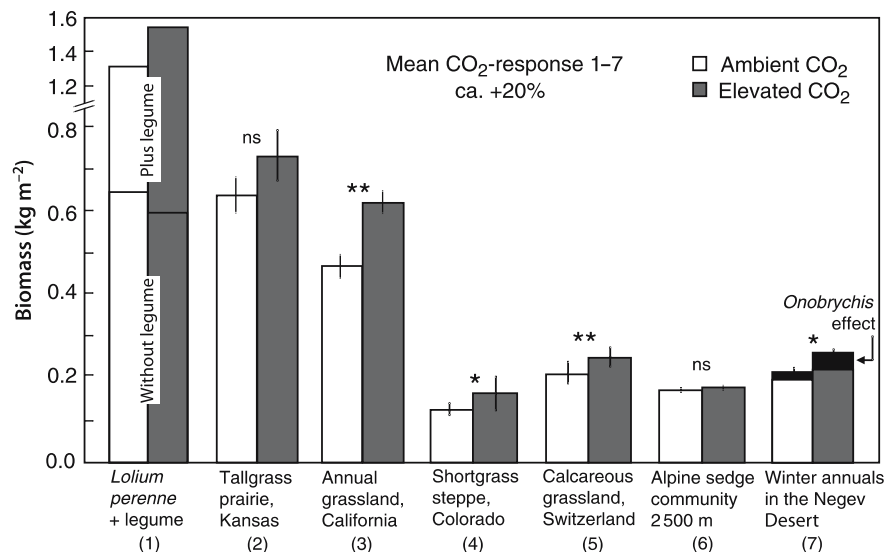
Grassland biomass responses to elevated CO₂ reported in the literature (Körner 2002) are clearly related to the fertility of the test conditions as well as to soil water availability. In mesic grasslands, CO₂-induced biomass increases are greater under more fertile conditions (e.g., Hebeisen et al. 1997). Alpine grassland seems to be an exception, since there was no positive growth response to elevated CO₂ even when mineral nutrients were added (Schäppi and Körner 1996). In native and semi-natural grasslands with no fertilizer amendments (Fig. 2.1), the seasonal biomass response to elevated CO₂ appears to be more pronounced in dry years, as a result of the CO₂-induced stomatal reduction of transpiration. This indirect water relations response to CO₂ enrichment increases leaf and canopy-level water use efficiency, extends the effective growing season in drier grasslands, and enhances nutrient availability (Morgan et al. 2004a). Most grasslands are characterized by periods of water shortage (Stephenson 1990; Campbell et al. 1997) and thus experience this indirect water relations benefit. A serious constraint on the usefulness of grassland biomass data produced under elevated CO₂ is the extrapolation of these indirect CO₂ effects to future environments because such water relation responses to CO₂ may not be seen in reality. At the landscape scale, reductions in leaf conductance to water vapor will lead to a drier and warmer atmosphere, which in turn would increase evaporative losses. Warmer future ambient temperatures will enhance such

evaporative losses, while predicted higher humidity in some locations might reduce them (IPCC 2001). The final outcome will depend on complicated interactions between the atmosphere and the biosphere that are difficult to predict, and will vary geographically. Thus, much of the presumed direct CO₂ effects on grassland biomass (Fig. 2.1) are in fact indirect water relations responses (Morgan et al. 2004a) that will have to be corrected for future atmospheric humidity conditions and humidity driven biosphere/atmosphere feedback – a major forthcoming challenge for modeling.

With these caveats, the seasonal gain in harvestable biomass of seven different grassland systems is between 0% and 30%, with the Californian grassland showing the largest and the alpine the smallest response. Removing the CO₂-induced moisture effect on biomass, the remaining effect will most likely be smaller than +10% for a doubling of CO₂ in most cases. Here and in the following, it is important to distinguish between net biomass accretion (what is left for harvest at peak season or after a season) and the total biomass which had been produced during a year, irrespective of whether it was preserved or had been recycled i.e., lost before harvest. The latter is called net primary production (NPP), and is much larger than, and not to be confused with, the standing stock of biomass.

Mature forest trees have been exposed to elevated CO₂ only in a few cases, with the majority of data coming from young trees in enclosures. A particularly valuable source of data has come from trees growing around natural sources of CO₂ (Miglietta et al. 1993; Amthor 1995). Oak trees (*Quercus ilex*) grown around natural CO₂ springs in Italy, showed a significant stimulation of tree ring growth during their years of re-growth after coppicing (Hättenschwiler et al. 1997), very similar to the responses seen in scrub-oak after fire (Dijkstra et al. 2002). Such re-growth situations after complete losses of above

Fig. 2.1. A comparison of biomass responses to elevated CO₂ in 6 natural grassland ecosystems (all grown on unfertilized ground) plus one artificial *Lolium perenne*/*Trifolium repens* stand (1). The prairie (2) and calcareous grassland (5) data are multi-year averages, with the positive effect largely introduced by dry years. Bars indicate plus/minus one standard error. References: (1) Hebeisen et al. (1997a), 5 cuts per year, 12 g N m⁻² a⁻¹, (2) Owensby et al. (1997), (3) Shaw et al. (2002), (4) Morgan et al. (2001), (5) Niklaus et al. (2001), Körner (2000), (6) Körner et al. (1997), (7) Grünzweig and Körner (2001)



ground structures represent a life phase for these trees with unlimited nutrient supply and ample space and light, conditions where carbon-assimilation may be the prime limitation of growth. Later, as stands close, the biomass relationships are re-established and excess nutrients are used up, the gain would be expected to vanish. Indeed, the gain in growth of Mediterranean oaks around CO₂ springs was greatly diminished compared to controls after about 25 years of growth under elevated CO₂ (Hättenschwiler et al. 1997).

Trees growing in older stands, which had reached a closed canopy before the onset of CO₂ enrichment may thus show much smaller CO₂ stimulation or more rapid re-adjustment to previous growth rates than was found in seedlings and saplings. Total foliage area (LAI) of fully developed canopies has not increased in response to CO₂ enrichment in any closed canopy system studied so far (Körner and Arnone 1992; Hättenschwiler and Körner 1996; DeLucia et al. 2002; Norby et al. 2003); hence, any growth response must derive from an enhancement of growth per unit leaf area.

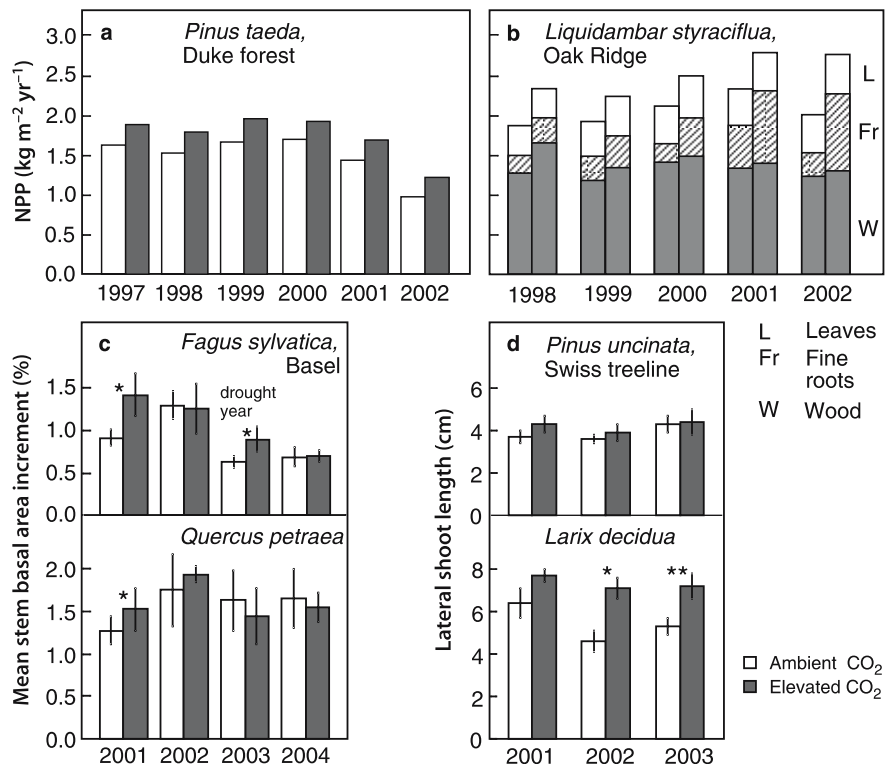
Three FACE experiments have been operating in tree stands starting with fully developed canopies: a pine (*Pinus taeda*) stand in the Duke forest in North Carolina, a sweetgum (*Liquidambar styraciflua*) stand at the Oak Ridge National Laboratory in Tennessee, and a mature multi-species deciduous forest near Basel, Switzerland. The young monospecific stands have shown a sustained increase in productivity in response to elevated CO₂, but the trajectory of growth response has differed.

Increased productivity in the pine stand has resulted in more stem growth and more leaf litter production (Hamilton et al. 2002; DeLucia and Moore 2005, Fig. 2.2a). Analysis of an additional plot at the Duke FACE site, however, suggested that an N limitation would cause this growth stimulation to disappear (Oren et al. 2001). Productivity in the deciduous sweetgum stand has been 22% higher in elevated CO₂, but the initial stimulation of aboveground growth disappeared after the first year (Norby et al. 2002; Fig. 2.2b). Instead, the additional carbon assimilated in elevated CO₂ has supported a large increase in fine-root production (Norby et al. 2004). The inherent difference in fine-root turnover rates in the pine and sweetgum stands (Matamala et al. 2003) may be an important determinant of whether a CO₂ stimulation of productivity results in increased growth or increased turnover, and this difference affects the long-term fate of C in the ecosystem.

The Swiss forest FACE experiment has been run for 4 years only, and the 30 m tall trees belong to several species, requiring a careful analysis of long tree ring chronologies to overcome obvious replication problems in the case of such large 'experimental units' and their restricted number. However, accounting for pre-treatment differences in vigor of individual trees (via tree ring analysis), the stem growth trajectory is similar to the one seen in the Oak Ridge FACE, showing a stimulation of radial growth in 100 year old beech in the first year which disappeared thereafter (Fig. 2.2c; Körner et al. 2005). Surprisingly, leaf photosynthetic capacity showed no down

Fig. 2.2.

A synthesis of in situ biomass responses of mature trees to Free Air CO₂ Enrichment (FACE). Net primary production (NPP) estimated from basal area increment, leaf litter collection, and minirhizotron analysis for a *Pinus taeda* (loblolly pine) plantation in North Carolina (DeLucia et al. 2005), and b for a uniform stand of *Liquidambar styraciflua* (sweet gum) in Tennessee, in this case separated by biomass compartments. Note the exclusive effect on fine roots (Norby et al. 2004). c Mean stem basal area increase (+ s.e.) in 2001–2004 of oak and beech at the Swiss Canopy Crane site (Asshoff et al. 2006). d as in c, but for shoot growth response to three consecutive years of free air CO₂ enrichment in 30 year old larch and pine trees growing at treeline (Swiss Alps, 2200 m). Mean shoot length was based on five lateral branches per tree ($n = 5$ trees per species/CO₂ level; Handa et al. 2005)



ward adjustment (Zotz et al. 2005), but soil CO₂-emission suggests enhanced carbon throughput in this system as well (Steinmann et al. 2004), which is in line with earlier findings for complex model ecosystems (Körner and Arnone 1992; Hättenschwiler and Körner 1996, 1998). The only case where woody plants showed a near homeostatic downward adjustment of photosynthesis under elevated CO₂ is the desert FACE experiment in Nevada (Hamerlynck et al. 2002). One may speculate that this has to do with a lack of significant below ground biological activity (e.g., mycorrhiza). A fourth FACE test established at the Swiss high elevation climatic treeline in 30 year old 1.5 to 2 m tall pines (*Pinus uncinata*) and larches (*Larix decidua*) also revealed an initial pine response, which disappeared by year three, but so far, a positive response in larch is persisting (Handa et al. 2005, Fig. 2.2d).

In summary, these data suggest a rather limited growth stimulation in mature trees, after the initial effect of a step-increase in CO₂ concentration is surpassed. However net primary production and the associated carbon turnover become enhanced in a high CO₂ environment, explaining in part the discrepancy between photosynthetic stimulation and biomass responses. The challenge for the future is to identify the fingerprints of enhanced carbon flows through undisturbed soils.

The available data for tall, closed canopy forests contrast with the significant stimulation often reported for seedlings or saplings grown under favorable experimental conditions. However, seedlings growing in deep forest shade, will take great advantage from the reduced light requirements for photosynthesis under elevated CO₂ under natural conditions, as was documented in situ for both a tropical (Würth et al. 1998) and a temperate forest (Hättenschwiler and Körner 2000). Under such conditions, elevated CO₂ is likely to affect tree recruitment in favor of particularly responsive species, and likely could affect future forest composition (see also the effect on lianas below).

2.2.3 Scaling from Growth to Carbon Pools

Great care is advised when translating such plot-based data into landscape carbon gains (Amthor 1995). At these larger scales the mean residence time of carbon per unit land area influences carbon stocks. If trees would grow faster and mature earlier, tree turnover would be greater, but not necessarily the mean C-storage in biomass. In fact, a faster forest rotation may reduce the forest C-pool. There is evidence for accelerated maturation in pine trees grown in elevated CO₂: cones were produced earlier and in greater masses than in controls (LaDeau and Clark 2001). The above described transient nature of tree growth responses to elevated CO₂ and the contribution of CO₂-induced water savings, which may in part be artifacts, because of a lack of atmospheric feedback, set rather stringent limits to expected growth stimulations

in a CO₂-rich world. Accelerated development may reduce mean forest carbon stocks (Körner 2003b, 2004), but enhanced C-turnover may also feed more carbon into the humus compartment, a rather uncertain projection, given the high demand for nitrogen and other minerals to form the complex humus aggregates.

Thus, an important message to users of experimental findings is that growth or productivity, i.e., a rate of carbon incorporation, as they are documented in some cases, should not be confused with the amounts of carbon stocked per unit land area. It is the latter which matters for sequestering carbon away from the atmosphere. In terms of carbon storage policy, a high stocking rate (e.g., old growth forests) is desirable rather than a faster forest rotation, as it may become facilitated by elevated CO₂ in plantations on fertile ground. Such growth stimulations, however, can add to the substitution of fossil by renewable fuels and products.

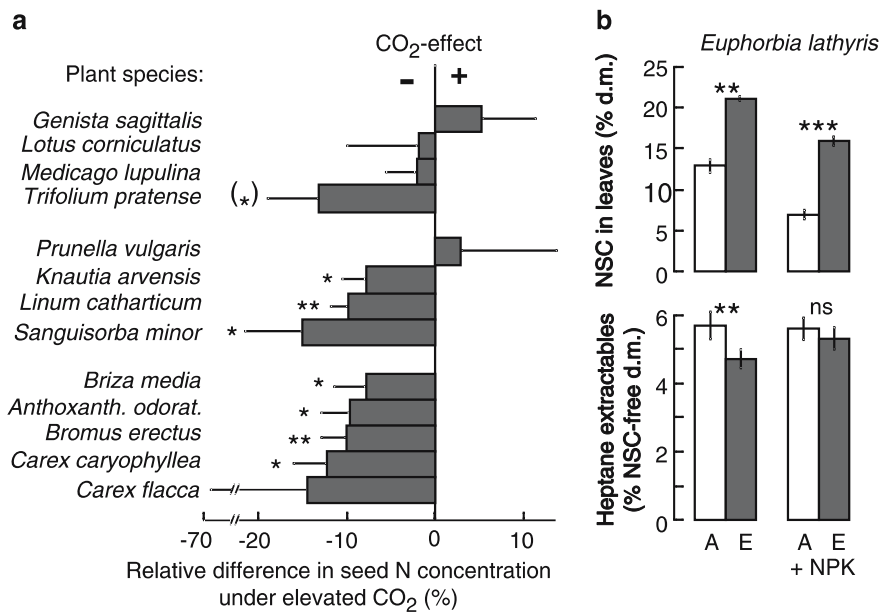
2.3 Carbon to Nutrient Ratios and Consumer Responses

2.3.1 The C to N Ratio Widens

It has been documented many times that exposure of plants to elevated CO₂ causes an increase in non structural carbohydrate concentrations (NSC; e.g., Körner and Miglietta 1994 for natural CO₂ springs, underlining the long term nature of this response) and a reduction in leaf nitrogen concentrations (Cotrufo et al. 1998; King et al. 2004). However, N-depletion is not a universal effect and often is a dilution effect caused by NSC accumulation, disappearing on an NSC-free dry matter basis. In tissues other than leaves, such changes have been seen less frequently. But seeds have also been found N-(protein)depleted in plants grown under elevated CO₂ under natural growth conditions (Fig. 2.3a), and in wheat when not heavily fertilized, with far ranging nutritional consequences (see below). Secondary compounds do respond as well, but in unpredictable direction (Penuelas and Estiarte 1998). An increase in desired mobile carbon compounds could be an asset. For instance the rubber tree might be expected to produce more latex and thus channel excess carbon assimilates in this non-structural biomass compartment. A growth chamber test with a relative of the rubber tree, *Euphorbia lathyris*, one of the so-called Diesel-plants, from which one hopes for fossil fuel substitutes, ended with a big surprise (Häring and Körner 2004). Elevated CO₂ significantly reduced latex production (Fig. 2.3b), unless plants received a lot of N-fertilizer. So far, stem wood produced under elevated CO₂ has not yet been found to contain less N or more NSC. Hence the idea that a widening of the C/N ratio in wood could allow more wood carbon to accumulate in the landscape with a given N supply has so far not been supported by data.

Fig. 2.3.

Elevated CO₂ influences plant chemical composition. **a** Relative difference in seed nitrogen-concentration under elevated compared to ambient CO₂ concentration in a calcareous grassland community (Thürig et al. 2003). **b** Effect of elevated CO₂ on non-structural carbohydrate concentration and concentration of heptane extractable hydrocarbon (latex) in *Euphorbia lathyris* leaves (Häring and Körner 2004)



2.3.2 Consequences for Herbivory, Decomposition and Plant Nutrition

A shift from protein to carbohydrates or more generally a wider C/N ratio is commonly considered negative for consumers (herbivores) and litter break down (decomposition). Some animals feed at equal rates and thus have reduced protein uptake rates, some feed less when faced with the N-depleted food, others compensate by feeding more, and others shift to other host plants. One important conclusion is that animals behave differently when given a choice of food plants (for reviews see Lincoln et al. 1993; Kinney et al. 1997). Reduction in forage quality due to CO₂ enrichment is a common theme in grassland CO₂ enrichment work (Owensby et al. 1996; Milchunas et al. 2005), and will likely have important consequences for many grazers. Altered grazing of CO₂-enriched forage may also feed-back on forage quality since re-growth tissue often differs in quality from non-defoliated tissue (Milchunas et al. 1995), and ultimately interacts with the environment to determine plant community composition. The change in seed quality (Fig. 2.3a) propagates effects to the next generation, but seedling success did not reveal strong influences when tested. Cereal grains, besides the nutritional effect as such, had been found to be of reduced baking quality in cases where elevated CO₂ was applied without extra fertilizer (e.g., Kimball et al. 2001).

Initial thoughts that leaf quality changes may translate into litter quality changes and a slowing of decomposition have not been supported by the majority of tests (O'Neill and Norby 1996; Norby et al. 2001; but there are a few exceptions). Effects may depend on the maturity of the test system and timing of the trial. Another key aspect is the export of excess carbohydrates to rhizo-

sphere microbes, which then become competitors for nutrients (e.g., Zak et al. 1993) and may even draw down productivity (Díaz et al. 1993; Hättenschwiler and Körner 1996; Shaw et al. 2002).

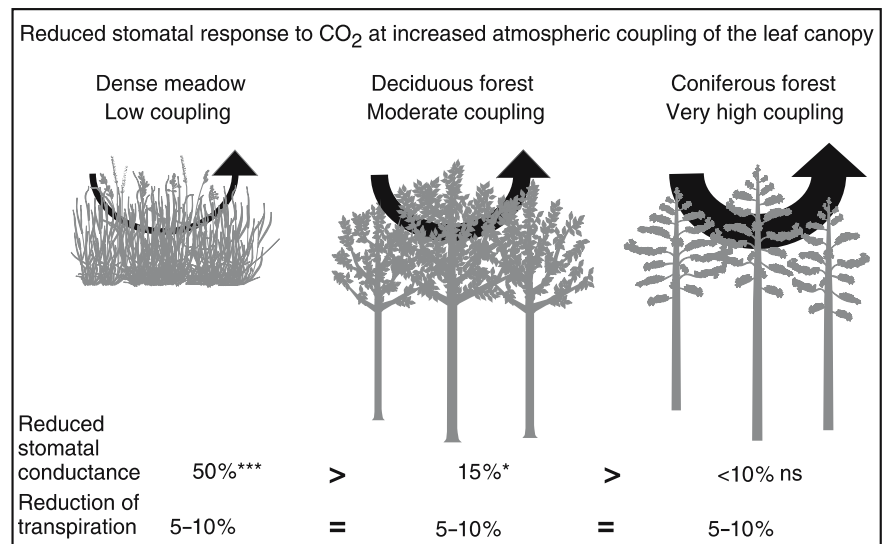
2.4 Plant Water Relations and Hydrological Implications

As briefly addressed in the biomass section, elevated CO₂ influences plant water relations through its effect on stomata. In turn plant water consumption influences soil moisture and atmospheric humidity, both feeding back on plants. Soil moisture feedback can be controlled and documented, or even simulated experimentally, but atmospheric feedback cannot. Hence all assumptions on influences of atmospheric CO₂ on hydrology depend on the nature of this feedback, which needs large-scale climate models to estimate. We recall, that between 65 and 70% of all vapor loss from vegetated land masses passes through leaf stomata (Maniak 1988; Gerten et al. 2005), thus causing any CO₂-driven effects to have substantial impact on the water balance.

Currently available data for natural ecosystems suggest a remarkable balance between stomatal responses and aerodynamic resistance which operates in a way so that water savings for a doubling of preindustrial CO₂ (ca. 550 ppm) are surprisingly similar for grassland, deciduous forests and conifer forests, despite large differences in stomatal responsiveness (Fig. 2.4). Although, signals differ a lot with species, with some responding strongly and others not at all, average stomatal conductances in grassland and crops may drop by 30 and 50% of controls (Knapp et al. 1996; Lauber and Körner 1997; Ainsworth et al. 2003; Kimball et al. 2002; LeCain et al.

Fig. 2.4.

A synthesis of water relations responses to elevated CO_2 for three types of vegetation. Round arrows symbolize the degree of canopy ventilation (a distillate from various sources, references in the text)



Stomatal responses to elevated CO_2 can influence atmospheric humidity as air masses move across the continent

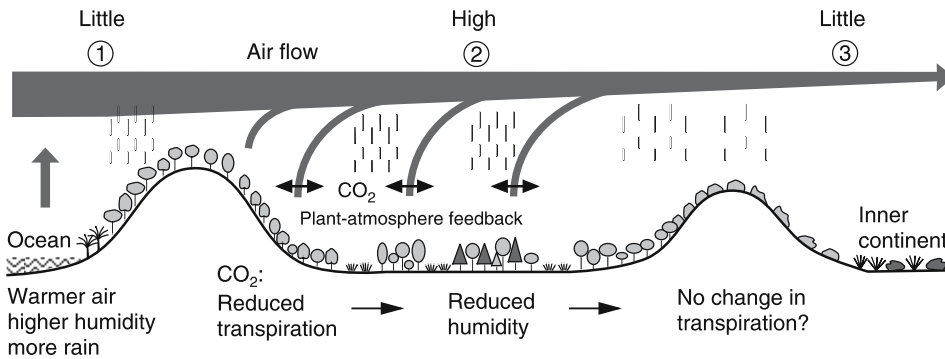


Fig. 2.5. Schematic landscape scale vegetation-atmosphere interaction resulting from stomatal responses to elevated CO_2 (Fig. 2.4). Coastal regions (1) are exposed to ocean driven atmospheric humidity (no or little vegetation-climate feedback). As air masses move across the continent, they take up moisture from transpiring vegetation, but based on available experimental data 5–10% less (Fig. 2.4) when elevated CO_2 reduces stomatal opening, with cascading downwind consequences for humidity (2) which feed back on transpiration to a point, where transpiration becomes very low in the semiarid continental interior (3) with minor vegetation influence on the atmosphere. Horizontal arrows symbolize regions of intense CO_2 -driven interactions between vegetation and climate

1993; Bunce 2004). In deciduous forest trees, signals average at around -20% (Saxe et al. 1998; Medlyn et al. 2001). It was a big surprise that none of the adult conifers ever tested produced the theoretically expected stomatal signal, which means, if there is a response, it would be within measurement error, i.e., smaller than 10% (e.g., Barton et al. 1993; Pataki et al. 1998; Ellsworth 1999).

This sequence of responsiveness at the stomata level is the reverse of atmospheric coupling, with dense grassland most strongly decoupled and conifers very well coupled to air circulation. Actual water flux studies in non-chambered grassland (e.g., Stocker et al. 1997) and cereals (e.g., Pinter et al. 1996), in deciduous forest trees (Wullschleger et al. 2002; Hungate et al. 2002; Cech et al. 2003) and in conifers (Schäfer et al. 2002), almost all arrive at seasonal savings between 5 and 10%, more close to 5%. Such a uniform effect is good news for model pa-

rameterization and is in line with an earlier proposition of such a balance of stomatal and aerodynamic controls of transpiration (Meinzer and Gantz 1991; Meinzer et al. 1993). Effects have been larger in some closed or semi-closed systems in which atmospheric coupling may have been enhanced, (e.g., Owensby et al. 1997). At the canopy scale, a best current guess is a reduction of evapotranspiration in this range, yet, without accounting for atmospheric feedback, which will reduce the effect. So, a realistic signal for hydrological considerations may be a 5% reduction in transpiration for twice pre-industrial CO_2 concentrations, irrespective of plant functional type. It is noteworthy that for plants it matters *when* these savings happen. Otherwise small differences in water consumption can improve drought survival. In wet conditions they may also enhance runoff. An important consensus from experimental results is that effects are stron-

gest under high humidity and decline rapidly as the vapor pressure deficit exceeds 10–15 hPa (Wullschleger and Norby 2001; Cech et al. 2003), an observation confirmed by earlier measurements in trees around natural CO₂ vents (Tognetti et al. 1996). Transferred to a landscape or continental scale, any reduction of vapor loss will change atmospheric moisture loading, which in turn, would affect (increase) vapor loss from vegetation (Fig. 2.5).

2.5 Stress Resistance under Elevated CO₂

Exposing plants to elevated CO₂ can have beneficial effects under conditions of stress such as water shortage and air pollution, but it can also diminish frost resistance.

Since stomates lose less water for a given amount of CO₂ absorbed when CO₂ concentrations are elevated, plants may do better under drought. More than 100 controlled experiments have explored this field and nearly all found drought mitigating effects of elevated CO₂ (e.g., Tolley and Strain 1984; Hibbs et al. 1995). However, as several authors have shown (e.g., Samarkoon and Gifford 1995; Volk et al. 2000) the secondary effects of high CO₂ on soil water (as discussed above) exert a strong confounding influence, particularly in pot studies with limited rooting volume. Wullschleger et al. (2002) consider the actual benefits in the field as minor. In the desert FACE experiment in Nevada, it was the moist period which permitted the greatest CO₂ effect on shrubs and none during a drought period, somewhat dampening perspectives for a greening of dry lands in a high CO₂ world (Smith et al. 2000). No conclusive benefits for Mediterranean shrubs around CO₂ springs could be detected during drought (Tognetti et al. 2000), but crops grown under FACE profited more from elevated CO₂ (in relative terms) when passing through a drought (Conley et al. 2001). Future research will have to clearly separate effects of soil moisture savings from actual drought × CO₂ effects.

In the light of the greater carbohydrate supply of leaves grown in elevated CO₂ (including osmotically active sugar), it came as a surprise that frost resistance declines in plants exposed to a CO₂-rich atmosphere. This was found independently in plants as different as a temperate herbfield community (Obrist et al. 2001), Australian eucalypts (Lutze et al. 1998) and Douglas fir (Guak et al. 1998). The changes may be within the natural safety margin (Repo et al. 1996) and roughly match predicted global warming, but nevertheless affect one of the basic determinants of global plant distribution.

Elevated CO₂ concentrations have also been shown to mitigate the impact of ozone and other airborne pollutants, in part by reducing diffusive uptake (stomata) and in part by compensating damage (reviews by Sullivan 1997; Volin et al. 1998; Poorter and Perez-Soba 2001). A combined O₃ × CO₂ FACE experiment with aspen confirmed these earlier findings and showed that certain

realistic ozone levels may offset positive CO₂ effects (Isebrands et al. 2001). In summary, CO₂ enrichment has the potential to mitigate certain environmental stresses.

2.6 Biodiversity Effects May Outweigh Physiology Effects

We want to close this brief assessment by highlighting the key significance of species identity for the long-term outcome of atmospheric CO₂ enrichment (see also Potvin et al. 2007, Chap. 9 of this volume). Beyond the well known differential influence of elevated CO₂ on C₃ and C₄ species, recent studies have revealed a far more subtle differentiation of species that does not relate to any conventional groupings of plants into functional types and for which we often have no plausible explanation. We will illustrate this problem with a few examples.

2.6.1 Hydrology Implications of Elevated CO₂ Depend on Species Abundance

Imagine a mixed forest in a catchment, with some species saving water under elevated CO₂ and others not. This had been documented in a pine-sweetgum forest in North Carolina (*Liquidambar* responding, *Pinus* not; Schäfer et al. 2002) and in a deciduous forest in Switzerland (*Carpinus* responding, *Fagus* not; Cech et al. 2003). The relative contribution of these species to the total forest canopy will determine whether the forest is saving water and how much. Furthermore, if one species saves, their non-saving neighbors may profit, which will alter the competitive balance and is most likely to induce a long-term change in community structure.

2.6.2 Biodiversity Effects on Forest Carbon Stocking and Grassland Responses

The longest term CO₂-enrichment experiments to date, the one in a wetland ecosystem, a sub-estuary of the Chesapeake Bay (Maryland; Hymus et al. 2003), all other grassland CO₂ studies (some examples in Fig. 2.1), the two forest FACE experiments in North Carolina and Tennessee, but also two newer tree FACE experiments in Switzerland (Fig. 2.2), clearly demonstrate that CO₂ exerts species specific effects. The two US forest FACE studies, for instance, arrived at similar responses of net primary production, but in the case of pine, the additional biomass largely ended up in stems, whereas in the case of sweetgum, it ended up in fine root turnover.

As mentioned in Sect. 2.2, accelerated growth may enhance tree turnover and lead to a lower rather than greater steady state C-pool in the landscape. One functional type of plants, lianas, the life cycle of which often

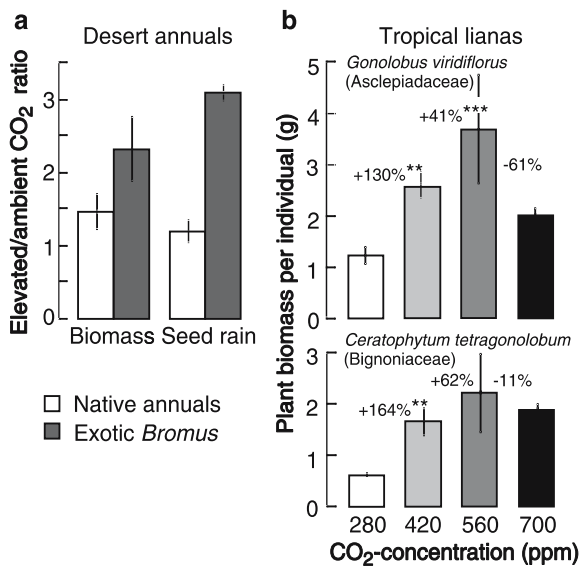


Fig. 2.6. Biodiversity–CO₂ interactions. **a** Mojave Desert native winter annuals and the exotic *Bromus madritensis* ssp. *rubens* (Nevada desert FACE, Smith et al. 2000). **b** the plant functional group of lianas. Bars indicate plus/minus one standard error (data by Granados and Körner 2002)

commences in deep shade, turned out to be particular responsive to elevated CO₂ (Granados and Körner 2002; Fig. 2.6). This has to do with a generally greater relative effect of elevated CO₂ on photosynthesis in deep shade. In the case of lianas, however, this stimulation greatly enhances their chance to reach the top of the forest. Well known to be the major driver of forest dynamics in the humid tropics (Schnitzer and Bongers 2002), such a greater vigor of lianas may cause the whole system to become more dynamic and store less C because trees do not live as long (Körner 2004). Demographic evidence suggests that such a process may be under way in Amazonia (Phillips et al. 2002) and had recently been reported for Panama as well (Wright et al. 2004). This example illustrates that there is no straightforward way to predict forest responses to elevated CO₂ from photosynthetic response curves without accounting for such biodiversity effects.

Similar examples have been shown in non-forest systems. For instance in the Mojave desert, an exotic annual *Bromus* grass species responds more strongly to CO₂ than native annuals (Fig. 2.6) enhancing the risk of fire (Smith et al. 2000). In the Negev winter-annuals' productivity (Fig. 2.1), it was a single species' response, which drove the whole community response. In the Colorado shortgrass steppe, recruitment of a single species under elevated CO₂ was largely responsible for a 41% production response (Morgan et al. 2004b). What if these species had been absent or were studied alone? Quite clearly species identity and species abundance have a major influence on the impact of elevated CO₂ on ecosystems.

2.7 Summary and Conclusions

Experimental CO₂ research with plants and whole ecosystems has made it clear that there is no straightforward relationship between the generally observed stimulation of leaf photosynthetic rates by elevated CO₂ concentrations and growth or productivity. The large number of tests with a broad spectrum of species and growth conditions have made it obvious that the extent to which greater availability of carbon to plants will translate into more structural growth depends on nutrient availability, either directly or via soil moisture conditions. The realism of projections derived from experimental works thus depends on the realism of nutrient and water regimes provided during tests (Körner 2003c). For the vast majority of non-agricultural ecosystems it seems that resources other than CO₂ control growth and productivity to such an extent that CO₂ concentrations above current levels exert little or no long-term stimulation. The major influence of atmospheric CO₂ on biota comes in (1) via differential responses of plant taxa or plant functional groups, (2) effects on water relations, and (3) soil feed back induced by greater C-input, the latter least understood.

Biodiversity effects have been found to be significant, with single species or plant functional types potentially driving whole system responses, and with no good explanations to date why this is so. The example of enhanced vigor of tropical lianas illustrates that functional group responses may in fact reverse the stimulatory effect of CO₂ enrichment into a reduction of carbon stocking in the single greatest biological C-reservoir on the globe. Water feedback may mimic growth stimulations in experiments, which may not be seen in reality when landscape wide feedback by climate and climatic changes are accounted for – a major future challenge for modelers. Nevertheless, the hydrological implications of elevated CO₂ are still a key global change aspect. Among the greatest surprises emerging from experimental works is that the differential responses of leaf stomates seen across taxa seem to level out to a common ca. 5–10% reduction of water loss at the ecosystem scale (evapotranspiration), a signal largely produced during humid periods.

Soil feedbacks other than through moisture include consequences of greater root turnover and microbial stimulation, but whether there will be a long term net input into the recalcitrant humus C pool is still very uncertain. Humus formation also strongly depends on nutrients, N in particular, and thus, competes directly with plant production and new C-input.

Overall, experimental CO₂ research has led to a wider appreciation of feedback constraints at the ecosystem level and the significance of plant taxa for ecosystem behavior (Fig. 2.7). At the ecosystem level, shifts in the presence and abundance of species may outweigh CO₂ effects seen at leaf or single species level. Taken together,

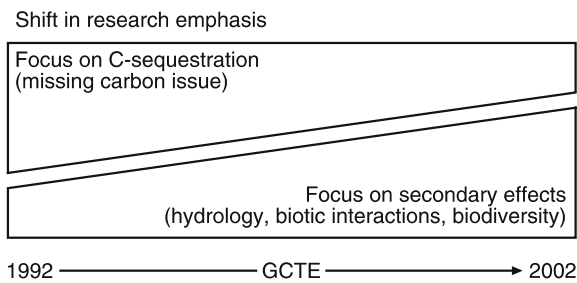


Fig. 2.7. The shift in research emphasis during the GCTE decade

the experimental findings suggest very cautious projections of CO₂ fertilization effects seen in short term tests with nutrient rich systems. Given that the few tests which used lower than current CO₂ (pre-industrial) concentrations as a reference to current or future concentrations revealed the strongest CO₂ effects (Fig. 2.6), the world may have seen or is midway into the most effective phase of CO₂ effects on biota, with a further rise perhaps exerting less additional effects. However, it will take many decades for the past and ongoing CO₂ effects to materialize, for instance, in the form of new plant assemblages.

Major questions to be explored in future biological CO₂ research are:

1. The translation of greater ecosystem carbon through-flow (growth rate, productivity, soil carbon fluxes) into steady state carbon pool sizes (biomass carbon, soil humus). CO₂ experiments revealed a lot of evidenced for enhanced carbon flux under elevated CO₂, but they are intrinsically constrained in estimating related changes in C-stocks. A worthwhile arena to be explored empirically is ecosystems of varying fertility, which exhibit contrasting carbon turnover for reasons unrelated to elevated CO₂. What are the mechanistic links between rates of carbon turnover (both at annual and centennial time scales) and the related pool sizes of biologically tied up carbon?
2. What are the long term consequences of plant species or functional type specific responses to elevated CO₂? It was a major outcome of GCTE related experimental research that biodiversity effects can outweigh physiology based 'average' plant responses at community level, and these consequences need to become focal areas of both further experiments and modeling. Based on this insight, it seems imperative, that future test systems include aspects of biodiversity, also in the light of the enormous costs involved.
3. There is an urgent need to implement realistic feedback between plant and ecosystem water relations under elevated CO₂ and atmospheric feedback in models. This is an arena where regional climate modeling and experimental research have to merge. Given the extent to which secondary effects of elevated CO₂ on water relations affect biomass responses and the

potential hydrological implications, we need to arrive at a clear separation of direct, photosynthesis driven CO₂ effects and indirect, water driven CO₂ effects, which reflect certain climatic conditions.

4. Among the many secondary effects of exposing plants and ecosystems to enhanced availability of carbon, those on herbivory, mycorrhiza and rhizosphere food webs and all sorts of other interactions between plants and other organisms will have to remain focal areas.

A grand vision from an experimental point of view, would be an international research consortium which taps resources representing a small fraction of outer space research funding in order to establish three major forest research facilities, one in the boreal zone, one in the temperate zone and one in the tropics. These facilities would test complex forest responses to our future atmosphere, capitalizing on the experience accumulated over the last decades on simpler test systems. These large scale tests would employ the latest CO₂ enrichment technology, applicable for tall and diverse tree stands; would gradually elevate CO₂ concentrations, provide the needed canopy access technology; take a broad interdisciplinary approach; and guarantee long test periods under common protocols. They would represent international focal points of experimental global change research and tap resources from national partner agencies, which otherwise may continue to be diluted into smaller scale enterprises.

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