



Tansley review

Plant CO₂ responses: an issue of definition, time and resource supply

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Summary

Key words: carbon, ecosystem, elevated CO₂, growth, nutrients, productivity, soil.

In this review I am drawing attention to some constraints and biases in CO₂ enrichment experiments and the analysis of data in the literature. Conclusions drawn from experimental works differ when the data are grouped in a way such that the relative frequency of test conditions does not determine the emerging trends, for instance unrealistically strong CO₂–‘fertilization’ effects, which are in conflict with some basic ecological principles. I suggest separating three test conditions: uncoupled systems (plants not depending in a natural nutrient cycle) (I); expanding systems, in which plants are given ample space and time to explore otherwise limited resources (II); and fully coupled systems in which the natural nutrient cycling governs growth at steady-state leaf area index (LAI) and fine root renewal (III). Data for 10 type III experiments yield rather moderate effects of elevated CO₂ on plant biomass production, if any. In steady-state grassland, the effects are water-related; in closed tree stands, initial effects decline rapidly with time. Plant–soil coupling (soil conditions) deserves far greater attention than plant–atmosphere coupling (CO₂ enrichment technology).

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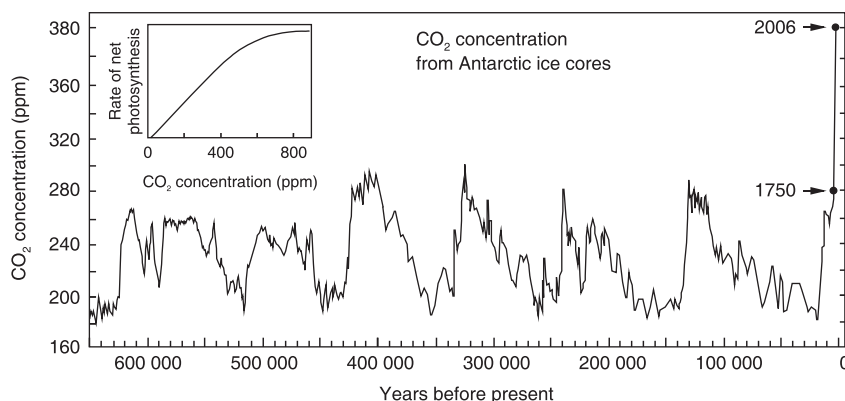


Fig. 1 The two 'icon type' diagrams for plant responses to elevated CO₂: the past 650 000 years' CO₂ concentration as extracted from Antarctic ice cores (combined data from Petit *et al.*, 1999 and Siegenthaler *et al.*, 2005) and the schematic response of leaf net photosynthesis of C₃ plants to rising ambient CO₂ concentrations.

I. A traditionally scarce resource becomes abundant

The effect of elevated CO₂ on plants has been the topic of several thousand scientific articles and approx. 120 reviews, *c.* 10% of which appeared in *New Phytologist*, so why another one? I felt it would be worthwhile to draw attention to some conceptual problems in experimental design and literature analysis. Much of what we believe we know today reflects the frequency distribution of test conditions, which thus deserve a careful evaluation.

The two most important and unquestioned components of global change which affect terrestrial biota are: (i) land transformation and the associated losses of soils, habitats for wild organisms, and the loss of and invasion by organismic taxa; and (ii) the chemical composition of the atmosphere, with increasing concentrations of compounds such as CO₂, CH₄ and N_xO_y and the associated climatic implications. While global land transformation is patchy, with complete losses of natural inventory and/or productive capacity in one place, and pristine remnants and/or highly productive areas elsewhere, the compositional changes of the atmosphere and their consequences reach all corners of the planet. While some of the chemical components released to the atmosphere through human activities may be rated as pollutants, CO₂ has been the basic resource for life for as long as eucaryotic photosynthesis has existed, possibly > 2.5 billion yr (Tolbert, 1994; Knoll, 2003; Giordano *et al.*, 2005); hence its sudden and rapid increase plays an exceptional role.

Over long geological periods, CO₂ was a major component of the atmosphere (> 5%). It dropped rapidly to < 1% in the Silurian age when oxygen arrived at close to current concentrations, just before life started to conquer the land (Berner, 1990). The second period of atmospheric CO₂ depletion occurred during the Devonian-Carboniferous explosion of terrestrial plant life, which ended *c.* 300 million yr ago, when concentrations had fallen to close to current values, coinciding with the Permian glaciation. For most of the (warm) Mesozoic, CO₂ concentrations were much higher than today and then dropped dramatically a third time in the Tertiary (Pagani

et al., 2005), when most modern plant genera evolved. At the Oligocene-Miocene transition, 20–25 million yr ago, CO₂ concentrations became, and since then stayed, so low that the C₄ pathway of photosynthesis became evolutionary advantageous, and evolved in 19 angiosperm families (Hatch, 1992; Ehleringer & Monson, 1993; Sage, 2004). Low CO₂ concentration rather than drought seems to have been the dominant driver (Pataki, 2002), although fire frequency has also been suggested as a cause (Keeley & Rundel, 2005). For the last *c.* 20 million yr, terrestrial plant evolution was codriven by the optimization of the use of its ever scarce 'staple food', CO₂. Most species that are dominating the current biosphere evolved under CO₂ concentrations of *c.* 240 ppm according to ice core data for the last 650 000 yr (Fig. 1). The current anthropogenic rate of atmospheric CO₂ enrichment thus comes as a rather novel experience to modern plant life, and the current *c.* 380 ppm exceed anything plants have probably had to deal with since at least the late Tertiary (Pearson & Palmer, 2000; Crowley & Berner, 2001).

One of the most striking pieces of evidence showing that plants do well with less than half the current CO₂ concentration comes from the peak of the last glacial period, only 18 000 yr or *c.* 180 tree generations ago, when the CO₂ concentration was *c.* 180 ppm: the currently existing *c.* 250 000 species of higher plants did so well during this period in their warm refugia that they made it into the current epoch. Compared with this glacial period, plants have already experienced more than a doubling of atmospheric CO₂ concentrations. Over geological periods, plants have 'learned' to cope with very low CO₂ concentrations. How will plants cope with the abrupt advent of the new planetary diet we are offering them today?

In this review, I will focus on plant growth responses (with a particular emphasis on trees), although elevated CO₂ affects almost any facet of plant life, including the interaction with other organismic groups. Since this field has been reviewed previously and at least 15 statistical treatments such as meta-analysis have been offered (Table 1), my main emphasis will be to discuss the meaning of the emerging response patterns in the context of how the data were obtained.

Table 1 A selection of reviews and conceptual papers on plant and ecosystem responses to elevated CO₂

General reviews	1, 2, 3, 4, 5s, 6, 7, 8, 9s, 11,
Agricultural plants	12, 13, 14s, 15, 16,
Grassland	17, 18, 19, 20, 21,
Trees and forests	22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 11,
Aspects of photosynthesis	32, 33, 34, 35, 36s, 37, 38s, 39s, 40,
Plant respiration	41, 36s, 42, 28,
Plant water	43, 44, 45, 46s, 47s, 48, 49, 15, 50, 21,
Plant nutrients	51, 36s, 52s, 37, 53, 38s, 15, 54s,
Below-ground responses	55, 56, 57, 58, 59, 60, 61, 62s, 63, 64,
Temperature interactions	65, 4, 66, 67, 68s,
Tissue quality	69, 70, 52s, 11, 54s,
Competition and biodiversity	71, 72, 73, 74, 17, 46, 11, 75, 76, 77, 78,
Reproduction and phenology	79, 80, 7, 81,
Conceptual works	32, 82, 83, 84, 85, 86, 87

s, statistical assessments such as meta-analysis.

The list also includes synthesis articles of long-term studies or original articles, which include exceptional literature accounts.

1, Lemon (1983); 2, Long & Hutchin (1991); 3, Woodward *et al.* (1991); 4, Gifford (1992); 5, Poorter (1993) (s); 6, Amthor (1995); 7, Ward & Strain (1999); 8, Körner (2000); 9, Ainsworth & Long (2005) (s); 10, Nowak *et al.* (2004); 11, Körner *et al.* (2007); 12, Wittwer (1984); 13, Acock & Allen (1985); 14, Ainsworth *et al.* (2002) (s); 15, Kimball *et al.* (2002); 16, Kim *et al.* (2003); 17, Polley *et al.* (1997); 18, Körner (2002); 19, Niklaus & Körner (2004); 20, Lüscher *et al.* (2004); 21, Morgan *et al.* (2004); 22, Eamus & Jarvis (1989); 23, Norby (1996); 24, Jarvis (1998); 25, Körner (1998); 26, Saxe *et al.* (1998); 27, Ceulemans *et al.* (1999); 28, Norby *et al.* (1999); 29, Gielen & Ceulemans (2001); 30, Kerstiens (2001); 31, Beedlow *et al.* (2004); 32, Arp (1991); 33, Long & Drake (1992); 34, Preiss (1994); 35, Berry *et al.* (1994); 36, Curtis (1996s); 37, Stitt & Krapp (1999); 38, Peterson *et al.* (1999s); 39, Medlyn *et al.* (1999s); 40, Ghannoum *et al.* (2000); 41, Poorter *et al.* (1992); 42, Drake *et al.* (1999); 43, Eamus (1991); 44, Tyree & Alexander (1993); 45, Hsiao & Jackson (1999); 46, Wand *et al.* (1999) (s); 47, Medlyn *et al.* (2001) (s); 48, Poorter & Perez-Soba (2001); 49, Kergoat *et al.* (2002); 50, Bunce (2004); 51, McGuire & Melillo (1995); 52, Cotrufo *et al.* (1998s); 53, Hungate (1999); 54, Yin (2002); 55, O'Neill (1994); 56, Diaz (1996); 57, Paterson *et al.* (1997); 58, Tate & Ross (1997); 59, Arnone *et al.* (2000); 60, Treseder & Allen (2000); 61, Zak *et al.* (2000); 62, Norby *et al.* (2001) (s); 63, Pendall *et al.* (2004); 64, King *et al.* (2004); 65, Rawson (1992); 66, Cannell & Thornley (1998); 67, Kirschbaum (2004); 68, Zvereva & Kozlov (2006); 69, Lincoln *et al.* (1993); 70, Poorter *et al.* (1997); 71, Bazzaz & McConaughay (1992); 72, Possingham (1993); 73, Diaz (1995); 74, Körner & Bazzaz (1996); 75, Niklaus *et al.* (2001); 76, Navas *et al.* (2002); 77, Poorter & Navas (2003); 78, Reich *et al.* (2004); 79, Reekie (1996); 80, Ceulemans (1997); 81, Jablonski *et al.* (2002); 82, Loehle (1995); 83, Körner (1995); 84, Hungate *et al.* (1996); 85, Luo *et al.* (1997); 86, Sage & Cowling (1999); 87, Körner (2003a).

The indirect consequences of greenhouse gas emission on plants via possible climatic changes will not be dealt with here. Although these climatic changes may have profound effects on their own, I do not think their interaction with concurrent atmospheric CO₂ enrichment will cause CO₂ effects, on a global scale, fundamentally different from the ones we see in experiments in a current climate, given the broad spectrum of climatic conditions already covered in these tests (including substantial deviations from 'normal'). Effective interactions appear to go in any direction (Rawson, 1992; Olszyk *et al.*, 1998; Shaw *et al.*, 2002; Zvereva & Kozlov, 2006). Even in the coldest (alpine) site tested so far, a particularly warm season which permitted a 25% growth stimulation, did not enhance the *in situ* influence of elevated CO₂ (Schäppi & Körner, 1996). Temperature effects may come in via water relations, which will be discussed later.

II. Photosynthesis is not saturated at current CO₂ concentrations

The photosynthetic machinery of plants, particularly that of C₃ plants, is able to handle far higher than current CO₂

concentrations. C₃ leaf photosynthesis, which is responsible for c. 80% of terrestrial productivity and the build-up of > 95% of the world's biomass C pool of c. 650 billion tons (Lloyd & Farquhar, 1994; Roy & Saugier, 2001), saturates when CO₂ concentration approaches c. 1000 ppm, and just compensates ongoing leaf respiratory processes at 20–50 ppm CO₂ (depending on temperature). Hence, the relative influence of any given increment of CO₂ concentration declines with the absolute concentration. The greatest effect of CO₂ enrichment is in the initial, nearly linear response range (inset to Fig. 1). The rate of CO₂ uptake becomes particularly sensitive to CO₂ when photon flux density is just sufficient for photosynthesis to balance leaf respiration (the light compensation point). Elevated CO₂ can shift this point to lower light intensities, and hence permits plants to grow in deeper shade.

Experimental evidence almost univocally shows a stimulation of leaf photosynthesis when plants are exposed to elevated CO₂ (see References in Table 1). Deviations in CO₂ supply, as we create them experimentally outside the leaf by CO₂ enrichment, are not so uncommon inside the leaf, where the lag between photosynthetic demand and stomatal supply of CO₂ under permanently fluctuating light conditions causes

The fate of carbon in plants

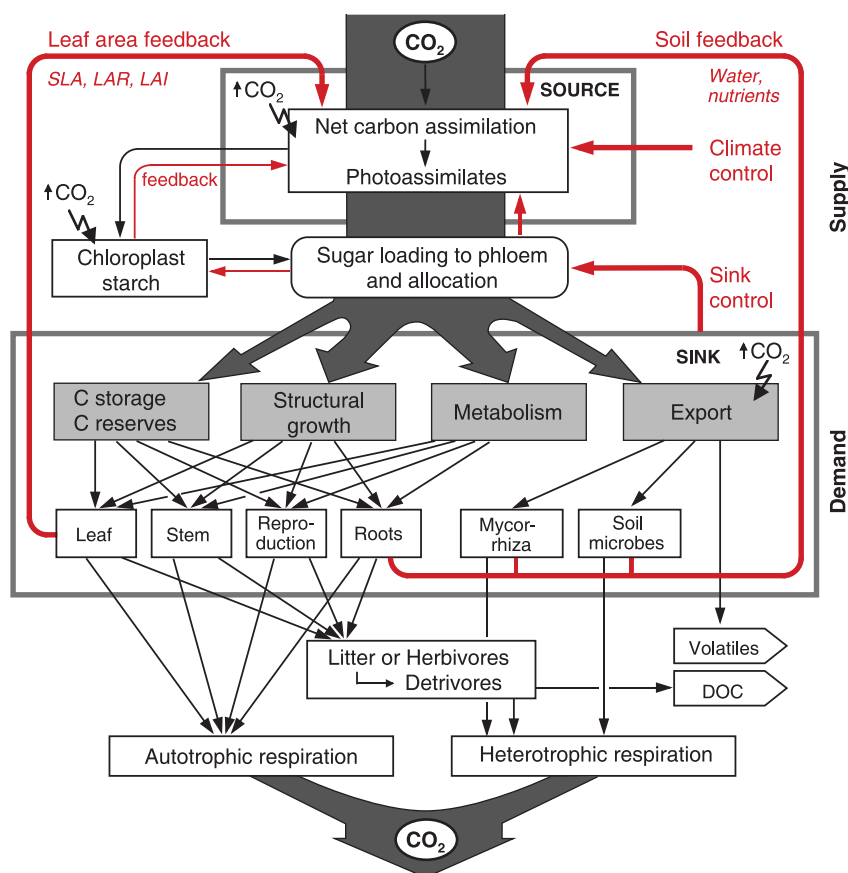


Fig. 2 The fate of carbon in plants. A schematic representation of uptake, allocation and export of carbon, with examples of feedback responses. (Modified from Körner (2003b) and reproduced with permission from Blackwell Publishing)

rapid changes in concentrations, and keeps the system 'trained' to deal with variation (Mott, 1990). Experiments with limited rooting space and with young plants have shown a certain degree of downward adjustment of photosynthetic capacity under longer-term exposure to high CO_2 concentrations (cf. Arp, 1991), but evidence for plants growing under near-to-natural growth conditions and for trees growing in the field does not reveal much reduction (Nowak *et al.*, 2004; Ainsworth & Long, 2005; Zotz *et al.*, 2005).

III. The fate of extra carbon

No doubt, more carbon is entering plants when leaves are exposed to elevated CO_2 . There are many avenues along which carbon assimilates can be processed, and only one of these is the production of plant biomass which can be harvested (Fig. 2). However, plants are not completely free in the directions of carbon allocation. Structural growth is controlled by a morphogenetic plan, by developmental stage and by the availability of resources other than carbon. Resource supply (light, water, soil nutrients) also drives carbon allocation into different plant organs such as leaves, stems, roots, storage and reproductive organs, but these organs also create their

own respiratory demand. The demand by microbial partners, mycorrhizas in particular, is another driver. Accretion of carbon in certain compartments depends on the longevity of these compartments (residence time). Hence, while all these processes need carbon assimilates in the first place, there is no straightforward mechanistic linkage between the rate of photosynthesis and the amount of carbon recovered in each of these compartments (Luo *et al.*, 1997). Crop physiologists were among the first to note with surprise the widespread mismatch between photosynthetic capacity of leaves and crop biomass production (Gifford & Evans, 1981; Wardlaw, 1990). Some high-yielding cultivars exhibit lower photosynthetic capacity than their wild ancestors, and hence hopes for engineering photosynthesis for better use of elevated CO_2 for higher crop yield seem unwarranted (Schimel, 2006).

The discrepancy between the almost uniform stimulation of leaf photosynthetic rates in proportion to a rise in CO_2 concentration and rather variable growth responses, from zero to massively positive effects, has puzzled researchers for as long as this research has gone on, and the puzzle has not been resolved (Nowak *et al.*, 2004) and approaches to understand it are advancing largely on theoretical grounds (Luo *et al.*, 2001). The main message from these many studies is that

there is no 1 : 1 translation of a photosynthetic CO₂ response into a growth response, and hence the diagram inset into Fig. 1 is not a very reliable guideline for predicting plant growth responses and the productivity changes these might incur. It is obvious from the examples shown in Fig. 2 that many other factors codetermine where carbon assimilates will go and stay for a while (the global mean residence of carbon in biomass is 10.4 yr; Saugier *et al.*, 2001). Note that Fig. 2 represents no aspect of timing or duration. The complexity of the scheme would be exaggerated if leaf and root longevity, rates of litter decay, turnover of reserve pools, and the timing and duration of carbon allocation to the microbial partners and plant reproductive events were included, and the whole scheme is under permanent adjustment as plants develop.

Because most of these drivers of carbon allocation in plants cannot be controlled, we are left with the net outcome of these processes, which will reflect the environmental and plant conditions we have chosen for our CO₂-enrichment experiments, the provision of resources other than carbon and the developmental stage of plants in particular. The hundreds of experiments that had been conducted differ in these conditions and, in order to arrive at a meaningful resumé, it is necessary to categorize results by these test conditions; otherwise, the results will reflect the frequency distribution of conditions under which the data were obtained (Körner, 2003a). For instance, if the majority of the data comes from plants which are young or widely spaced, or which grow on fertile ground, the overall analysis will always reflect the response of these categories (Körner, 1995; Loehle, 1995). A qualified stratification of the data available today is the centrepiece of any trustworthy analysis. In the next section I will suggest how one might arrive at a more balanced picture. There is no perfect recipe, though, but a separation in major groups of growth conditions seems indispensable, as difficult as this might be with the oft-scarce information provided. In methods sections, atmospheric conditions commonly cover more than 10 times the printing space of below-ground conditions, and 'exhaustive' statements such as 'grown on the university campus soil' are symbolic, while the actual weight of information is the other way round, should CO₂ effects be understood.

IV. Co drivers of plant growth responses to elevated CO₂

Like all other organisms, plants require a suite of chemical elements other than carbon to carry out metabolism and to grow. It has long been known that the ample availability of all these elements, plus sufficient water, light and warmth, causes carbon to become the remaining limiting resource, and elevated concentrations of CO₂ can cause a strong 'fertilizer' effect; hence the routine application of CO₂ enrichment in commercial glasshouse horticulture (Wittwer, 1984, see Bornemann, 1930 for one of the earliest accounts). Enhanced plant growth under elevated CO₂ can also be achieved by the dilution of

elements other than carbon (sometimes called increased nutrient use efficiency), but when this occurred this was commonly restricted to green foliage and was rarely reflected in litter signals (Norby *et al.*, 2001). If noncarbon elements in litter were depleted, this would slow down the nutrient cycle (negative feedback).

When plants grow in isolation and are allowed to expand their foliage and roots freely in all directions, the primary photosynthetic stimulation by elevated CO₂ becomes enhanced by compound interest effects, with more CO₂ causing more foliage, which in turn fixes more CO₂ and so on, theoretically endlessly if there were no ageing effects or space constraints. The maximum potential of unlimited plant growth stimulation by elevated CO₂ under such conditions may permit a quadrupling of biomass in young trees in 3–4 yr, as has been shown for widely spaced sour orange trees grown on soils treated with nutrient solution in a hot desert environment (Idso & Kimball, 1992). This is a useful reference for how far things can be pushed, but obviously is not a good model for predicting the response of trees in a forest.

Plants with a shorter life span and determinate growth, or plants that grow in closed canopies, have much less leeway to profit from such compound interest effects of elevated CO₂ concentrations, causing the net annual gain in biomass production for a 200 ppm increase or doubling of control concentration of CO₂ to remain below +50%, even under otherwise horticulturally optimized growth conditions, and the overall mean found in meta-analysis was around +30% per season for such test systems (Acock & Allen, 1985; Poorter, 1993; Curtis & Wang, 1998). Under standard agronomic field conditions optimized for high yield, the gains found for well-watered and fertilized wheat and rice averaged between +7 and +12% only (Kimball *et al.*, 2002). Water stress, while reducing absolute yield, may increase the relative stimulation by elevated CO₂ (see the later discussion). Responses of tree seedlings or cuttings during their 'weedy' initial life (Loehle, 1995) show similar responses to, or even larger responses than, herbaceous plants. Because such young trees contrast with nonwoody plants in that they can accumulate signals over a season of more than a few months, their responses may even exceed those seen in short rotation crops (Ainsworth & Long, 2005). These are good starting points to explore plant growth responses to elevated CO₂ under less ideal conditions, that is conditions as they mostly occur in the field, in wild plants in particular, but these conditions must first be defined in as simple a way as possible. At any given soil moisture, the following three main categories of growth conditions may serve this purpose:

- *Type I: a priori high abundance of major resources other than carbon – 'decoupled' systems.* This category includes plants receiving mineral fertilizer, plants which grow in recently disturbed soils that naturally release a lot of nutrients, plants inhabiting naturally fertile habitats (e.g. estuarine flood plains), plant regrowth immediately after fire or coppicing, or plants

grown in fresh forest gaps. In the main, this category includes conditions where plant growth is not tightly coupled to/or depending on a microbial rhizosphere food web but where plants have ready access to free and abundant soil nutrients.

- *Type II: conditions of aerial expansion: expanding systems.* This category refers to plants studied during a phase of life when available resources per unit land area (soil volume, aerial photon flux density) have not yet been fully explored, that is when the development of plants has not yet reached a steady state in terms of soil or air space exploration, root turnover, canopy expansion or litter production (expanding systems). This includes plants which grow without competition and in unrestricted space. All these conditions make otherwise limiting resources periodically highly abundant to plants. Space, both below and above the ground, becomes a resource in this sense. In fact, plants growing under such conditions experience type I conditions, while a soil chemical analysis, for instance, would not reveal luxurious conditions. Elevated CO₂ is likely to enhance the initial exploration of the available soil and air space.

- *Type III: near to steady-state nutrient cycle and full canopy development – ‘coupled systems’ (steady-state systems).* Growth under conditions where the ecosystem becomes largely self-supporting in terms of mineral nutrition, with nutrients in the soil solution reaching a minimum and nutrient addition rate by microbes (Ingstad, 1982) becoming the rate-controlling agent. Under these conditions, growth rates depend on the rate of recycling of organic material, substrate weathering and natural atmospheric input of mineral resources. Total fine root mass and leaf area index (LAI) reach a steady state (i.e. do not increase from year to year). Hence, ‘steady state’ only refers to foliage and fine root turnover and does not imply stability, nor does it suggest a sort of climax condition of succession. It simply means that the available space had been occupied and the nutrients required for further growth in the main come from inside the considered system (nutrient recycling).

Obviously there are no sharp boundaries between these three categories. While types I and III are relatively easy to define, type II conditions might be overlooked, because they describe conditions where a higher than sustainable supply in mineral nutrients or light comes into play indirectly, through insufficient exploitation of these resources per unit land area (either through low density or young age/size of plants, compared with the carrying capacity of the land). Other codeterminants of a CO₂ response of growth seem of far less significance. For instance, plant age may in fact be covered by category II (expanding systems). In experiments, young plants commonly have ample space to explore and operate a long way from steady state; hence it is very hard to separate a ‘true’ age effect from the confounding resource supply effect.

The most complicated situation is a combination of types II and III, that is when plants pass through type II conditions under experimentally elevated CO₂ and then enter type III conditions with the net outcome of the benefits under type II. The type II response will set the stage for the following type

III stage, no matter what effects CO₂ enrichment might have under type III conditions. In the real world, type II conditions are rare, and if they occur, have very short duration, because a ruderal, early succession flora would rapidly occupy any available space. Plants in deep forest shade may be an exception.

A few important, long-term CO₂-enrichment experiments in the field do not fit these categories well, and may thus be considered special cases: (a) the longest field test to date, the flood plain study in the Chesapeake Bay (Rasse *et al.*, 2005), a steady-state system by the above criteria, but ‘open’ (i.e. decoupled) in terms of nutrient supply; (b) a short rotation coppice poplar plantation (POPFACE), that is a fertile system prevented from arriving at steady state (Wittig *et al.*, 2005); (iii) the Swiss treeline free-air CO₂ enrichment (FACE), where isolated trees (expanding canopy) are growing under strong below-ground competition with a steady-state dwarf shrub heath (Handa *et al.*, 2005). The latter two may marginally fit type II, while the first a type I situation.

Compared with the influences of these growth conditions, the influence of the techniques of CO₂ enrichment (e.g. glasshouse, open top chambers (OTCs), FACE) appear almost negligible, but have been given great weight in meta-analysis of published data. Findings obtained in such different test systems do not differ qualitatively (Norby *et al.*, 1999), but even if they differ quantitatively, this is largely because these CO₂-enrichment methods are heavily confounded with the type of growth conditions. Glasshouse experiments are mostly done with young plants in fertile substrates (type I), OTC experiments often use young plants in disturbed soil (and, in the case of seedlings or cuttings of trees, start with type II conditions), and closer to steady-state systems are more likely to be explored by FACE. In the few cases where type III growth conditions have been applied in glasshouses or OTCs, the results did not differ from field trials without enclosures. In essence, I believe, the debate about the realism of CO₂-enrichment experiments has, in the main, been driven by technological considerations that account for comparatively minor influences on microclimate, rather than for the key subterranean covariables, which determine plant growth responses to elevated CO₂, as has been stressed in nearly all reviews of the subject (Table 1, see also Fig. 6). Badly designed enclosure systems can create climatic artifacts (e.g. a warmer interior), but these effects are usually still minor compared with the consequences of direct (type I) or indirect (density/age, type II) effects of the availability of resources other than carbon. Hence, the technology debate has overshadowed the required soil debate. Well-designed OTCs, the operation of which costs little compared with a FACE operation, have been discredited during this debate, while in many cases (particularly for low stature vegetation) they can provide just as good an understanding of CO₂ effects, provided soil conditions are realistic (Dijkstra *et al.*, 2002; Morgan *et al.*, 2004; Niklaus & Körner, 2004; Rasse *et al.*, 2005). For tall forests, unfortunately, we have no alternative to FACE (Pepin & Körner, 2002), but

in the forest understory, OTCs are perfectly suited, and even complete (flow-through) enclosures have been found not to affect the microclimate around ground vegetation in a dense humid tropical forest (Würth *et al.*, 1998).

There is growing awareness that the below-ground functional boundary of plants is not the root surface. Plants, very much like humans, depend totally on a microbial partnership, which is an integral part of their normal functioning (Högberg & Högberg, 2002; Högberg *et al.*, 2002; Read *et al.*, 2004; see also Table 1). Decoupling plants from this envelope (e.g. by fertilizer application) is like feeding a person by venous infusion, rather than letting *Escherichia coli et al.* do the job. Most of the world's biota are highly coupled systems in this sense. Luxmoore *et al.* (1986) stressed the CO₂ × microbial linkage 20 yr ago. Using forest tree girdling (Högberg *et al.*, 2001) and stable carbon isotope tracer signals fed into tree canopies (Steinmann *et al.*, 2004; Körner *et al.*, 2005), the rapid and rather direct coupling of the photosynthetic machinery in the forest canopy with the subterranean consumers of photoassimilates became obvious. About half of all CO₂ released from soil comes from very recent (a few days earlier) photosynthesis (Steinmann *et al.*, 2004; Tang *et al.*, 2005). It seems imperative that such linkages are intact, when plants are exposed to elevated CO₂. This is what 'coupling' is meant to emphasize (Körner, 2000; Nowak *et al.*, 2004).

Water has been disregarded in the above resource discussion, because its influence is a special case. Abundant moisture removes water-driven growth constraints, makes soil nutrients readily available, and may thus facilitate high absolute growth responses to CO₂ enrichment, provided other resources permit. However, elevated CO₂ also removes some of the moisture constraints as they commonly occur in the field, through its influence on stomatal conductance and the resultant water savings in the ground. If elevated CO₂ is permitted to influence soil moisture through reduced transpiration under otherwise unaltered atmospheric conditions, CO₂ enrichment may in fact mimic effects of better water and nutrient supply (Volk *et al.*, 2000). For biomass responses to elevated CO₂ in mesic grassland, this seems to be the major path of action, leaving us with the problem that we do not know whether an atmosphere that is dynamically coupled with land surface phenomena would counteract such water-savings effects by exerting greater evaporative demand (drier air, higher leaf temperature; Idso *et al.*, 1993; Amthor, 1995; Field *et al.*, 1995; Körner *et al.*, 2007). Water savings can almost fully explain relative biomass responses of grassland to elevated CO₂, with no additional photosynthesis-driven signal needed to explain the observed growth responses (Volk *et al.*, 2000; Bunce, 2004; Morgan *et al.*, 2004; Table 2a). This also explains why, contrary to expectation, C₄ plants have been found to profit from CO₂ enrichment (Samarakoon & Gifford, 1996; Owensby *et al.*, 1997). Separating such water signals from photosynthesis signals seems imperative for a conclusive interpretation of CO₂-enrichment trials.

V. Plant CO₂ responses as a function of time

The considerations discussed in the previous sections have deliberately been restricted to growth responses. Growth refers to the net accumulation of biomass in a given plant or group of plants over a certain period of time. In annual plants, this may be represented by the maximum biomass attained, or by the rate of growth by which a certain biomass is approached. In the first case, the harvest date is determined by plant phenology, in the second case by a defined lapse of time. The results commonly differ a lot, and hence there is a significant leeway for interpretation, and timing of census plays a significant role in the resultant signal size (Loehle, 1995).

In annual systems, there is a reset after each growth cycle in the course of an experiment, except if the new cycle is made depending on seed production of the previous cycle and if reproductive output was affected by elevated CO₂. Annual plants also have the experimental advantage that they enter the new (CO₂-enriched) life condition without a prehistory, except for influences on seeds or seedling performance. In perennial plants, CO₂ signals can accumulate. The effect becomes particularly strong in the case of woody plants, when the test is initiated in type II conditions. This phenomenon has been documented for young trees in several OTC experiments (Norby *et al.*, 1995, 1999; Centritto *et al.*, 1999; Spinnler *et al.*, 2002). In perennial grassland, such signal propagation is less likely even when the test starts from seed, because the half-life of organs is short and steady-state stand density is reached rapidly. I suspect this is the trivial reason why young trees have been found to be more responsive to elevated CO₂ than grassland and crops (Ainsworth & Long, 2005). In order to separate signal propagation from ongoing CO₂ stimulation, a careful growth analysis is required (Fig. 3). Should such a test system arrive at similar biomass after some years in both treatment and control, the relative growth rate of the high-CO₂ group must be even less for a while than that of the control group, in order to compensate for the initial stimulation (Centritto *et al.*, 1999; Fig. 3d). Transient responses as in Fig. 3(c) seem most likely, with the stabilization at a time when LAI and fine root density reach their maximum and compound interest effects become zero. In essence, the response in Fig. 3(c) represents a phase shift (timing) in development. Whether a CO₂ effect will be retained after the breakpoint will depend on the rate of nutrient addition (Oren *et al.*, 2001). In any case, the timing of a biomass census will strongly affect the result (Hättenschwiler *et al.*, 1997; Wittig *et al.*, 2005). In the example chosen for Fig. 3(c), the total effect would be 100% at census time 1, 20% at census time 5, and 2% at census time 50. Soil resources will determine the degree to which transients will depart from the solid line (dashed line in Fig. 3c, i.e. longer stimulation).

When perennial plants such as trees receive a CO₂ treatment after they have passed into the steady-state stage of LAI

Table 2 Grassland and forest test systems which have reached steady-state growth before CO₂ enrichment (a, b; type III systems) or approached it during CO₂ enrichment (c, i.e. expanding systems of type II)

Name of site (no. species/dominant)	Type of vegetation	Duration (yr)	Replicated (n)	Reference examples
<i>(a) Steady-state grassland systems (type III)^a</i>				
Kansas (> 12/3)	Tall grass prairie	8	3	Owensby <i>et al.</i> (1999)
Montana (35/3)	Short grass prairie	5	3	Morgan <i>et al.</i> (2004)
Swiss low (25/3)	Calcareous grassland	6	8	Niklaus & Körner (2004)
Swiss alpine (10/2)	Alpine grassland	4	12/4	Körner <i>et al.</i> (1997)
California (–/4)	Mediterranean annual	3	8	Shaw <i>et al.</i> (2002)
Nevada (> 12/4)	Desert annual/shrub	4	3	Smith <i>et al.</i> (2000); Nowak <i>et al.</i> (2004)
Negev (25/3)	Semiarid annual	1	3/6	Grünzweig & Körner (2001)
<i>(b) Steady state forest systems (type III)^b</i>				
Duke (1 +)	Conifer plantation	4 (10)	1/3/4	Oren <i>et al.</i> (2001); Schäfer <i>et al.</i> (2003)
Oak Ridge (1)	Deciduous plantation	6 (9)	2	Norby <i>et al.</i> (2004)
Basel (4)	Deciduous forest	4 (6)	1	Körner <i>et al.</i> (2005)
<i>(c) Examples of expanding young tree stands (type II systems)^c</i>				
Swiss tropical	15 species stand	0.3	2	Körner & Arnone (1992)
Italian CO ₂ springs	<i>Quercus ilex</i>	30	2	Hättenschwiler <i>et al.</i> (1997)
Florida	<i>Quercus</i> sp.	7 (10)	8	Dijkstra <i>et al.</i> (2002)
Tennessee	<i>Quercus alba</i>	4	4	Norby <i>et al.</i> (1995)
Wisconsin	<i>Populus</i> , <i>Betula</i> , <i>Acer</i> sp.	7 (9)	3	King <i>et al.</i> (2005)
Oregon	<i>Pseudotsuga menziesii</i>	4	2/3	Olszyk <i>et al.</i> (2003)
Sweden	<i>Picea abies</i>	4	3/6	Kostiainen <i>et al.</i> (2004)
Swiss lowland	<i>P. abies</i> , <i>Fagus sylvatica</i>	4	4	Spinnler <i>et al.</i> (2002)
Swiss montane	<i>Picea abies</i>	3	6	Hättenschwiler & Körner (1996)
Swiss treeline	<i>Pinus uncinata</i> , <i>Larix decidua</i>	3 (6)	5/10	Handa <i>et al.</i> (2005)

The number of species and years of operation refer to the references mentioned (and, in few cases, to pers. comm.). Tree model systems were included preferentially when they were sustained into steady-state LAI and/or were using unamended natural forest soil. See text for results.

^aThe longest test series, that of a *Scirpus* estuarine flood plain system, is a category in its own, because it is in a steady state but, as a result of its seasonal flooding and eutrophy, is a quasi-open system (Rasse *et al.*, 2005). The Nevada desert system includes shrubs. The winter-annual Negev desert system was included, although the test was not *in situ*, but in large (400 kg) containers filled with native Negev soil, a situation that is very close to natural for this ephemeral desert vegetation.

^bThese are the three sole test systems with closed forest canopy at the beginning of CO₂ enrichment. Years are given for the periods for which the required biomass/productivity data were available (in brackets, total duration by 2006).

^cAll these type II test conditions started with small isolated plants, either seedlings, cuttings or re-sprouts after coppicing or burning. Most examples reached close to steady-state LAI by the time of the final harvest, although plants were still very young and the experiments closed before stand self-thinning commenced. This does not hold for the shrub oak, boreal conifer and treeline experiments, where individuals remained isolated. Data from stands, which were re-cut during the experiment, were disregarded here. The Tennessee *Q. alba* stands had been thinned in year 3 'to optimize spacing' and the Swiss montane and Tennessee tests used two elevated CO₂ concentrations. Note that duration refers to season, which in the case of temperate montane, boreal or Mediterranean is 4–5 months yr^{–1}, in the warm temperate zone 6–7 months and in the tropics 12 months, that is, the potential maximum signal size per year is three times bigger than in a montane or boreal system.

and root turnover, compound interest effects (the initial ramp in Fig. 3b–d) will be small or absent. Accelerated nutrient foraging facilitated by greater assimilate supply may be one reason for an initial burst of growth. Such effects have been reported for all three forest-scale CO₂-enrichment experiments (Table 2b, Fig. 4). If, after such an initial phase, CO₂ enrichment causes a constant relative gain over time, the system would be driven in a sort of Fig. 3(b) scenario, which is highly unlikely (continued exponential growth). A more realistic case in nutrient-rich systems would be a constant

absolute gain, which actually means a diminishing relative stimulation with time (dashed line in Fig. 3c), but, mathematically, this depends on whether one uses total biomass or the increment per year only. The scenario in Fig. 3(c) was seen in *Quercus ilex* grown around natural CO₂ springs for 25 yr after the last coppicing (Hättenschwiler *et al.*, 1997), and in Florida scrub oak (B. Hungate, pers. comm.) following initial postfire stimulation (Dijkstra *et al.*, 2002). After a long enough time, it becomes impossible to separate the solid line response in Fig. 3(c) from that in Fig. 3(d).

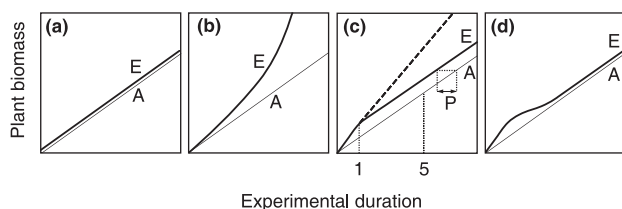


Fig. 3 A schematic representation of four different types of CO_2 responses of plants when CO_2 exposure is initiated at the seedling or rooted cutting stage (type II growth conditions). (a) No CO_2 effect; (b) continuous CO_2 effect combined with compound interest effects (expanding system), leading to exponential growth; (c) initial effects as in (b) but no further stimulation after completion of canopy and root volume expansion; (d) initial effect as in (b) but return to control biomass after completion of the expansive phase. (a) and (d) responses to a step increase in CO_2 may be very rare in expanding systems, but are possible in steady-state systems (d incurs a period of negative effects); (b) is impossible in nature, because it contravenes the law of limiting resources (except for short periods), so variants of (c) are most likely. Note that the constant difference between the two solid lines after the breakpoint in (c) results in diminishing relative responses with time. E, elevated; A, ambient CO_2 concentration; P, phase (time) shift in plant development.

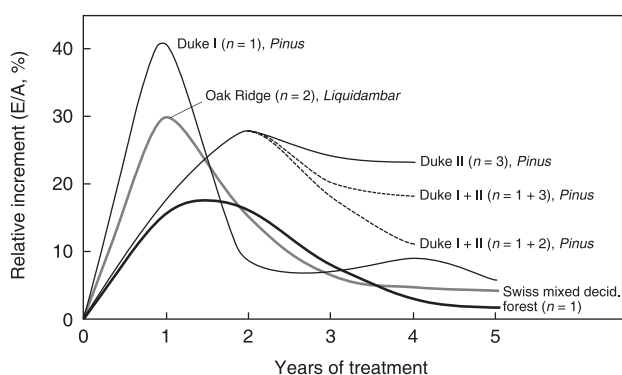


Fig. 4 Schematic above-ground growth responses of forest trees to elevated CO_2 in the three existing (type III) forest-scale CO_2 -enrichment experiments. E/A ratios (elevated vs ambient CO_2) are for either annual tree basal area (Swiss) or above-ground biomass increment or net primary production (NPP; other experiments), which does not affect the overall trend of strong initial and reduced later CO_2 responses. Duke I depicts the single free-air CO_2 enrichment (FACE) ring pilot study (Oren *et al.*, 2001), Duke II is for the replicated ($n = 3$) main experiment at Duke. Duke I + II offers the combined data for all four FACE rings at Duke using the data by Schäfer *et al.* (2003), with a variant (lowest dashed line, $n = 1 + 2$) without the single FACE ring that showed exceptionally high stimulation in year 4 for unknown reasons. The Oak Ridge data are from Norby *et al.* (2004), and the Swiss data are from Körner *et al.* (2005). For the sake of clarity, data points and error bars have been omitted, and trends were smoothed by hand.

CO_2 effects on plant communities that have already established close to steady-state fine root mass and LAI (canopy closure) before the test commenced cannot propagate previous CO_2 effects (the ramping in Fig. 3b–d), but they will always propagate their previous life conditions and life history

into the response obtained after a step increase of CO_2 concentration. Unfortunately, in the case of forests and in view of tree generation times, we have little alternative to an experimental step increase in CO_2 concentration, because any practical ramping would still be far steeper than the actual rise of CO_2 in the atmosphere of $1.5\text{--}2\text{ ppm yr}^{-1}$. Hence, CO_2 enrichment in these cases induces a step change in life conditions, which may cause initial over-reactions (Luo & Reynolds, 1999), followed by time-dependent adjustments to a new growth regime, as permitted by factors other than CO_2 . The only way to cope with such transitions from initial disequilibrium to new equilibrium conditions is time series analysis over as many years as possible (Fig. 4). Key to any such analysis is to account for individualistic or plot-specific growth signals by covariant analysis or standardization by growth before the treatment period (as can easily be achieved in trees using tree ring analysis; Norby *et al.*, 2001; Körner *et al.*, 2005; Asshoff *et al.*, 2006). Because there are only three steady-state forest CO_2 -enrichment experiments (referred to previous sections), this issue has not yet been widely discussed.

VI. Plant CO_2 responses per unit land area, a matter of definition

Most of the considerations discussed in previous sections focused on growth of individual plants or plant stands, based on raw data (biomass), simple to obtain and straightforward to analyse. A next step is accounting for productivity per unit land area, using a suite of approaches that require a lot of expert skills and usually remain mysterious to nonexpert readers. I noticed that, for the average reader, science journalist or politician, it makes no difference if a text refers to growth or production or net primary production (NPP) or net ecosystem production (NEP) or gross primary production (GPP). For most people, these are synonyms and refer to something one can touch or harvest. Scientists know that this is not the case. There may be little or no change in the annual increase in biomass stores (e.g. forest growth in the common sense) but substantial gain in productivity. By definitions developed during the International Biological Program (IBP) in the late 1960s, following Boysen-Jensen (1932), NPP refers to the annual accumulative amount of biomass produced per unit land area, be it present (harvestable) or not (i.e. consumed by animals, lost as litter or to symbionts etc. between census intervals; Roy & Saugier, 2001). NPP excludes respiratory losses by the living plant (*c.* half of all gross primary production), but it treats decomposed (metabolized) organic debris as 'produced'. It also treats sugars exported to mycorrhiza as 'produced'. So sugar, which had been respired in the plant body, is not treated as 'produced', but sugar exported from the plant and metabolized by external consumers is treated as 'produced'. Obviously, true NPP following this definition cannot be measured and what is published as NPP are approximations obtained by assessing at least changes in

standing crop biomass and adding litter production, which is not an easy task below ground. GPP cannot be measured either, but is commonly estimated via photosynthesis models. NEP is discussed later in this section.

It clearly makes a big difference in the context of elevated CO₂ research whether effects are expressed as biomass accretion ('standing crop' *sensu* IBP), NPP or GPP. When expressed as NPP, numbers include biomass, which has in fact disappeared, and when expressed as 'standing crop' this is the actual change in biomass-C pool size per unit land area. When expressed as GPP, this refers to a quantity of carbon, half of which was never structural biomass, but had been recycled immediately to the atmosphere. While GPP estimations are more of an academic exercise in this context, biomass and NPP can serve different purposes, and the most useful way of expressing CO₂ responses depends on the question one is trying to answer. Quite often, the two are either confused or it is taken for granted that readers would 'prefer' NPP, hence implying that NPP responses to elevated CO₂ are the more desirable quantity to be known.

This seems like narrowing the scope of biological CO₂ research to one of several aspects: (i) plant performance, that is plant fitness and plant life cycle responses to the new resource supply, with implications for biodiversity and organismic interactions (e.g. herbivory, symbiosis); (ii) understanding plant growth and biomass accretion (yield, biomass C stores); and (iii) ecosystem processes, C cycling and ecosystem C storage, which comes down to carbon in soil humus. NPP is one of the many drivers of soil humus formation. Although there is no straightforward linkage between soil humus stores and NPP, it needs NPP in the first place, should humus stores increase. It should be remembered, though, that ecosystems with very high humus C stores often exhibit very low productivity, and vice versa, and there is no C storage in humus without storage of other elements, N in particular. Hence, except for questions related to carbon cycling and humus formation, biomass and plant quality changes to elevated CO₂ are of greater interest than NPP, and under no condition should NPP be confused with either biomass carbon storage or total ecosystem carbon storage.

The choice of such expressions is not trivial, because it may even determine whether there is a CO₂ response or not. For instance, four FACE experiments with trees (two steady-state, two rapidly expanding) arrived at *c.* 20% increase in productivity (NPP), but there was no difference in above-ground standing crop biomass in the Oak Ridge FACE compared with controls (Norby *et al.*, 2004, 2005), and the other three differed widely in actual biomass increment. The GPP of one, a young poplar stand, reached +250% in the first year of CO₂ enrichment alone (Wittig *et al.*, 2005). The stimulation of GPP of the Basel forest FACE trees is in the order of +40% (based on canopy photosynthesis data by Zotz *et al.*, 2005), but the actual change in stem biomass increment was zero after 4 yr. The messages to the outside community (but not only) are almost certainly fatally confusing.

When the ecosystem carbon balance is of interest, the appropriate quantity is NEP, the net ecosystem productivity, which is the net flux of carbon across the ecosystem boundaries. Although there are other carbon flows than CO₂ (e.g. isopren emission or losses as dissolved organic carbon (DOC)), net CO₂ fluxes can be measured with sufficient accuracy using modern meteorological techniques that account for net vertical eddy flux and < 1 ppm resolution gas concentrations. The problem is that the release of large quantities of CO₂ in FACE experiments interferes with such techniques, and test areas are far too small to measure net ecosystem C fluxes in such experimental sites. Hence, net ecosystem carbon accretion or release needs to be estimated indirectly with stable carbon isotope techniques in both (!) treatment and control areas (VanKessel *et al.*, 2000; Lichter *et al.*, 2005), or by balancing estimates of NPP with estimates of respiratory fluxes (Schäfer *et al.*, 2003; DeLucia *et al.*, 2005), which incurs very large error terms that add up if one builds differences. In the case of forests, NEP includes a trivial and a delicate signal: the fact that trees accrete mass as they grow is trivial, while the net carbon balance of soils is not. The current global signal for soil carbon for a 35% departure from preindustrial atmospheric CO₂ concentration is in the order of 1–1.5 permille yr⁻¹ of mean organic C content of soils, *if* all globally 'missing carbon' were exclusively sequestered to soils. So, it is nearly impossible to assess realistic changes in humus carbon stores in CO₂-enrichment experiments by mass balance calculations (Hungate *et al.*, 1996).

VII. CO₂ effects on biomass carbon stores in forests depend on tree demography

Since trees store *c.* 85% of global biomass carbon, it is worth asking how CO₂ enrichment could enhance this C pool and how experiments can contribute to this question, that is, how a change in growth rate could translate into a bigger biomass carbon pool per unit land area. As mentioned earlier, it matters whether CO₂-driven growth responses obtained are derived from expanding or steady-state systems. In the case of grassland, steady state includes regular disturbance by grazing or cutting regimes, which are part of the annual recycling process. Typical natural steady-state grassland systems are prairie, steppe or alpine grassland. Sustainable (extensive) rangeland grazing systems may also fall into this category. In the case of forests, steady state allows for self-thinning, but does not mean stable biomass, as is the case in grassland (if one considers long time series). Under 'steady state' as defined in this way, forests in essence increase their basal stem area per unit land area and lift their crowns by stem growth with the associated branch and large root biomass increments. This process is not linear, but passes through characteristic phases often represented by a sigmoid growth curve (Fig. 5), with only the initial part not in steady state, according to the above definition.

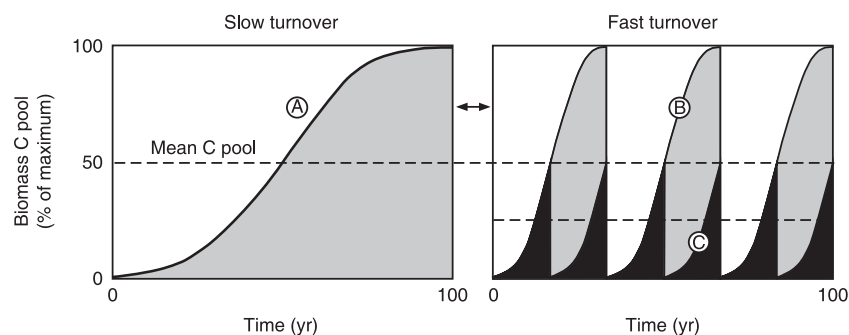


Fig. 5 Idealized growth curves of trees growing at slow (a) and three times as fast (b and c) rates. In (a) and (b), trees grow to equal individual mass, while in (c) trees are harvested in accordance with economic maximum-yield scenarios (rapid rotation plantation, higher overall yield per unit of time). The horizontal dashed line indicates the mean biomass storage over the whole life cycle, which is not different in (a) and (b), but which is lower in (c). These single tree growth curves also apply to stands of equal age. In a commercial forest landscape, all tree/stand age classes would ideally cover equal fractions of land area (sustainable forestry). In a pristine natural forest, all age classes may be randomly mixed or occur patch-wise, depending on disturbance regimes.

Should elevated CO_2 stimulate tree growth, trees would commonly pass through these curves faster, that is they would reach the plateau earlier in time, irrespective of whether the stimulation was restricted to the initial phase or continued life-long (Fig. 3; Beedlow *et al.*, 2004). The amount of carbon stored in tree biomass in a given landscape will depend on the fraction of trees falling into the biomass classes of this growth curve. In managed systems, the time of harvest will determine the pool size, that is, the duration of carbon in the system. In systems with natural gap dynamics, the age (and size) at tree falling will control the size of the carbon pool.

Hence, contrary to the still widespread belief, growth rate and biomass storage are not, or not positively, correlated at a landscape scale (Fig. 5). Quite often, and depending on growth stage, they are negatively correlated. When growth rate is tripled, as in the right panel of Fig. 5, but trees are harvested at equal size (biomass), the mean pool size over time remains unchanged. When trees are harvested in their most productive phase (as is the case in fast rotation plantations), the yield over time can be strongly increased (as long as soil nutrients can cope with it), but the carbon pool size is actually diminished. Hence growth or yield should never be confused with carbon storage; this is very similar to the economy, where cash flow (equivalent to growth rate, carbon cycle) should not be confused with capital (in this context, biomass C stores). When a stimulation of tree growth by elevated CO_2 does occur, this will enhance tree dynamics and perhaps yield, but not automatically long-term carbon sequestration. However, a growth stimulation would permit existing forests to reach the high storage age more quickly, a phenomenon that has been called 'buying time' (in terms of greenhouse effect mitigation). Such transitory increased C pools would only exist to the extent that trees are not harvested or are senescing earlier. In fact, if such acceleration would occur at present, we would export a carbon release wave into the future, when a greater fraction of forests will enter the harvesting or senescent age.

In other words, carbon storage in biomass on a landscape scale is an issue of tree demography and not a question of growth rate. CO_2 -enrichment experiments do not have the power to predict future tree demography, and hence are inherently unsuitable to assess trends in biomass carbon stocking in a CO_2 -rich world. However, they are suitable for studying a large number of key plant responses to elevated CO_2 , including changes in ecosystem carbon fluxes, biodiversity and, last but not least, plant growth responses in their own right. Many of these responses may indirectly contribute to a more realistic picture of carbon sequestration by the biosphere and they certainly contribute to a better mechanistic understanding of plant and ecosystem carbon relations and how these are coupled to nutrient and water relations. Many people have been misled to believe that growth and NPP are synonyms of carbon storage. This is how much of the research in this field has been reported in the media, an arena that deserves more careful use of jargon on the part of scientists.

VIII. Biomass responses to elevated CO_2 in steady-state and expanding systems

For all the reasons discussed in the previous sections, the following account will be restricted to biomass responses. Because CO_2 effects under type I and II conditions have been reviewed extensively before (Table 1), the main emphasis of this account will be on responses under type III growth conditions. Type III studies that were carried out for at least 3 yr and which offer comparable biomass responses are rare, but, nevertheless, the results of these studies should come closest to what might actually happen to the vast majority of ecosystems outside agriculture and forest nurseries (Table 2). Thus the criteria by which works have been ranked as type III are steady-state canopy (LAI) and fine root turnover, and a natural nutrient cycle (no fertilizer added). Thus, steady state by no means implies 'natural', stable or late successional. This

restricts the analysis to seven grassland and three forest studies out of hundreds of studies world wide.

Steady-state grassland systems (Table 2a)

Kansas. No response in wet years, significant gain in dry years, largely because of the responses of Cyperaceae and forbs. There was clearly no disadvantage of C_4 grasses, most likely because they profited similarly from soil moisture savings as C_3 taxa.

Montana. The mean +40% response in biomass production was the result of one C_3 grass species (*Stipa comata*) and was clearly driven by moisture savings, which permitted greater seedling establishment.

Swiss lowland. No response in wet years, but a significant response in dry years, arriving at a mean +18% yield, largely because of Cyperaceae. The effect was almost completely explained by soil moisture effects of elevated CO_2 .

Swiss alpine. Clearly no response, irrespective of season or nutrient addition. This site at 2500 m elevation has a dense, late successional heath operating under naturally low nutrition and at 25% reduced partial pressure of CO_2 . It came as a surprise that nutrient addition, which doubled biomass, did not facilitate a CO_2 effect over 4 year.

California. No overall CO_2 effect, when tested across all combinations with warming, nutrient addition or watering treatments. When tested alone, CO_2 enrichment exerted a 33% peak biomass increase. Surprisingly when CO_2 was added to any of the other treatments, it reduced their stimulating effect drastically.

Negev. The peak season biomass response was +17%, but resulted almost exclusively from the response of a single species out of 25 (one out of five legume species, *Onobrychis crista-galli*). Without *Onobrychis*, which is the most mesic element in this system, the CO_2 effect was zero.

Nevada. This desert system operates far from complete ground cover, and hence may expand. There was a small CO_2 effect on a native, but a massive effect on an exotic *Bromus* ($\times 2.3$) because of the combination of density and individual growth (+50%) responses; forbs were stimulated by +40%. In shrubs, there was no response in relatively dry years but a massive effect in an exceptionally wet year (shoots extension $\times 2$). Root responses to CO_2 were negative (fewer roots).

Summary for steady state grassland

Of the seven steady-state grassland systems, three are from a temperate summer-dry climate, three are Mediterranean/

semiarid grass-shrublands, and one is a humid alpine grassland. The data show a clear influence of soil moisture and an overarching effect of few very responsive taxa, which are commonly of a more mesic nature. In no case were legumes as a group positively, and C_4 grasses as a group negatively, affected (no change in the $C_3 : C_4$ ratio was found around geological CO_2 vents in South Africa; Stock *et al.*, 2005). The desert system, which is in fact a potentially expanding system, shows moisture responses contrasting the temperate grassland. The completely undisturbed, late successional alpine grassland was unresponsive irrespective of temperature (and associated moisture) or nutrients. Below-ground responses show no consistent pattern and go from negative (desert) to moderately positive (proportional to above-ground responses). Grassland biomass responses to elevated CO_2 are strongly affected by CO_2 -induced water savings (Morgan *et al.*, 2004). Whether such soil moisture effects and the associated biodiversity effects occur in the future will depend on concurrent climatic change. A photosynthesis-only driven CO_2 effect seems rare/small in these late successional systems. Once CO_2 -induced moisture effects are accounted for, there remains no direct CO_2 effect on growth, and hence the overall effect could have been simulated with a watering treatment alone (Volk *et al.*, 2000). The consistently higher responsiveness of mesic taxa (taxa known for their preference/high abundance on moist ground) which drive the overall system responses seems to reflect these moisture savings.

Steady-state tree stands (Table 2b, Fig. 4)

Duke. Results for the pilot project ($n = 1$) and the replicated project ($n = 3$) and their combination ($n = 4$) are considered jointly. All tree stands show a strong initial basal area/NPP response (up to 30%), which declined after 2–3 yr. In 1999–2000 the fourth and fifth years, the combined effect ($n = 4$) was $\approx +18\%$, but this was the result of a single treatment/control pair, which showed a response two to eight times as high ($\approx 41\%$) as the other three plots (≈ 5 – 17% ; Schäfer *et al.*, 2003). Without this plot-pair, the effect is down to $\approx +10\%$ in 2000. The stimulation is the result of faster stem growth and there is no LAI effect, but more needle litter production.

Oak Ridge. As in the Duke system, trees showed a strong initial growth response, which declined already after year 1 and disappeared later, but fine root production and peak season fine root biomass remained stimulated, and associated below-ground metabolic activity was enhanced. Hence NPP is consistently increased, but above-ground biomass does not profit from elevated CO_2 . LAI and leaf litter production are unaffected.

Basel. Because trees are twice as tall (30–35 m) in this natural mixed forest as in the other two experiments, the replicated units are not plots ($n = 1$) but individual trees ($n = 10$, each

covering 30–100 m² of canopy) belonging to four different species. As in the other experiments, there was a strong initial stimulation in tree basal area, but in one of the four species only, and by year 4 the growth response of this species disappeared and the response across all trees became zero (when accounting for individualistic pretreatment tree ring growth). Root data are still missing, but below-ground metabolism is clearly enhanced. LAI and leaf litter production are unaffected.

Summary for steady-state tree stands

All three experiments, which started to enrich forests with CO₂ after canopy closure had been reached, revealed a strong initial stimulation of growth or NPP, followed by a subsequent decline. LAI remained unaffected and photosynthetic capacity showed no downward adjustment. At Oak Ridge the remaining signal is annual fine root production, while at Duke, stems are the prime responsive unit, but the means strongly depend on one particularly stimulated CO₂ plot. Duke trees also started to reproduce earlier, and hence development was accelerated. Trees in the Basel FACE lost sensitivity to CO₂ by year 4, but there is an indication that moisture savings play a role in dry periods as in grassland, and tree species show contrasting responses. The assumed reason for the rapid decline in biomass responses to elevated CO₂ in all three cases is growth limitation by the natural nutrient cycle. In the Duke pilot study ($n = 1$), a split-plot fertilizer treatment facilitated a sustained CO₂-driven basal area stimulation. All three sites show enhanced below-ground metabolism under elevated CO₂. Given the rather different sites, tree taxa, tree age and growth conditions, the patterns seen across these tests are surprisingly similar. Taken together, these results suggest far less than, or even none of the expected long-term stimulation of above-ground forest growth or productivity in a 160–200 ppm CO₂-richer future, except under high mineral nutrition.

Expanding tree communities (Table 2c)

In the 10 cases listed in Table 2c of young tree growth under close to natural soil conditions, trees approached a closed canopy (initiated from juvenile, seedling or cutting stage). Five of these cases show no effect of elevated CO₂ on tree growth or tree biomass accumulation per unit ground area: the montane, boreal and treeline evergreen conifers and the tropical model system. A number of other type II studies have found no growth stimulation by elevated CO₂, when no extra nutrients were provided (Barton & Jarvis, 1999; Winter *et al.*, 2000; Maroco *et al.*, 2002). In the other cases, CO₂ responses were restricted to the first year or first few years, with compound interest effects propagating these initial differences in canopy development. The final difference thus depended on the years to canopy closure and time of harvest. The

cumulative biomass effect after 3–7 yr is even smaller than what would be expected from capitalizing the initial separation of the ambient vs elevated canopy expansion in response to CO₂ (if there was any). In most cases, massive stimulation of below-ground activity was found in elevated CO₂, and root system expansion was accelerated (faster exploration of available space). These results are relevant for future forest gap dynamics and recruitment. Maybe gaps will close faster in a CO₂-rich future.

Because of species differences in responsiveness, elevated CO₂ will select for more responsive taxa during this phase, at the disadvantage of slower ones (Tangley, 2001; Körner, 2004). However, such differences depend on growth conditions. The only CO₂ experiment ever conducted with trees on contrasting soils (Fig. 6) revealed a clear soil \times species interaction, further modified by nitrogen deposition. In this case, calcareous vs acidic soil, taken from sites where *Fagus sylvatica* and *Picea abies* co-occur, did not affect the joint final biomass or LAI of the two taxa. However, soil type determined whether spruce became dominant or not, and, on acidic soil, elevated CO₂ even had negative effects on the growth of beech.

IX. Conclusions

In this review I have tried to highlight major codeterminants of plant CO₂ responses, which need to be accounted for should the resultant trends not just reflect the abundance of a certain type of study (Pendall, 2002). The results of 20 experiments, with examples for plants growing under conditions of a close to natural nutrient cycle in > 160 ppm above ambient CO₂, yield a different picture of CO₂ biomass effects from what had previously emerged from not separating expanding from steady state, fertilized from unfertilized, or young from mature plant stands. These types of experimental conditions appear to be far more important than whether plants grow in enclosures or not.

In natural or seminatural grasslands, which depend more on shallow soil moisture, CO₂ effects are strongly tied to water savings (Morgan *et al.*, 2004), so the direct CO₂ effect via photosynthesis becomes overshadowed and responses cannot be directly compared with tree responses. Another important distinction between grassland (or crop) and tree biomass responses is that annual responses can accumulate and thus accelerate with time in young expanding tree canopies, but not in plants with a determinate seasonal growth cycle. This 'young trees effect' (aerial expansion) should not be confused with a greater intrinsic responsiveness of trees to elevated CO₂.

Trees show similar positive initial responses to a step increase in CO₂ concentration when they grow in isolation during their earliest life phase, compared with trees whose crowns had formed close canopies before the experimental step increase in CO₂ was applied. However, in young expanding trees these initial responses can propagate for some time in the form of compound interest effects as stands develop

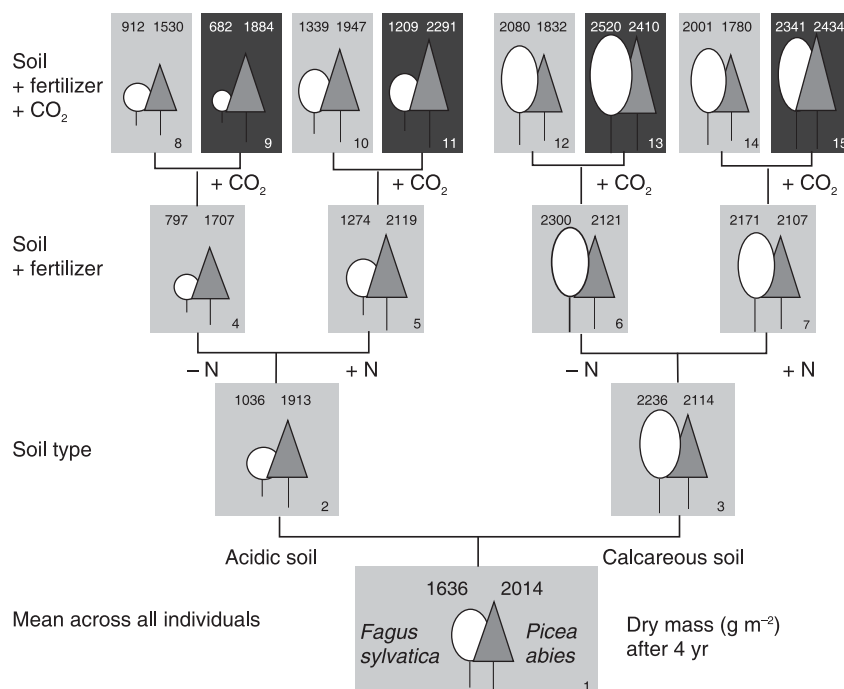


Fig. 6 A schematic, stepwise representation of the results of the only CO₂-enrichment experiment so far which employed two different native soils (on which two test species co-occur naturally) in a fully replicated ($n = 4$) CO₂ × N treatment over 4 yr (CO₂ × species × soil × N interaction). Had only one soil type and only one species been employed, rather different conclusions would have been drawn depending on the design. While beech may be outcompeting spruce on calcareous soil under elevated CO₂ in the long run (e.g. box 12 or 13), the opposite is true on acidic soil (box 8 or 9), illustrating biodiversity effects in response to a complex environmental × CO₂ interaction matrix. The results underline the overarching significance of soil conditions and species identity in CO₂ research (from data in Spinnler *et al.*, 2002).

(and soil nutrients permit), while in steady-state canopy situations, the LAI is set and does not permit such self-propagation of the initial signal. In not a single case was steady-state LAI increased under elevated CO₂, and in a few cases there was even a slight trend for reduced steady-state LAI under elevated CO₂. In all cases, in young expanding systems in particular, below-ground carbon metabolism was found to be accelerated when tree canopies experienced elevated CO₂ (Körner & Arnone, 1992; King *et al.*, 2004; Steinmann *et al.*, 2004). There is a consensus in the literature that the nutrient cycle sets the ultimate limit to a carbon-driven, long-term stimulation of plant production (Finzi *et al.*, 2002; Hungate *et al.*, 2006). Soil conditions and plant species exert an overarching influence on experimental results (Fig. 6) and thus deserve more attention in experimental design. To affect the global carbon cycle, growth and productivity responses must translate into greater landscape-wide biomass and soil humus stores, which is a matter of long-term forest and soil dynamics and land use practices, not really accessible by CO₂-enrichment experiments at the timescales needed (Lichter *et al.*, 2005).

Studies conducted under conditions in which plant growth was coupled to the nutrient cycle, and particularly those in which plants had reached a steady-state canopy development, revealed far smaller (often zero) influences of elevated CO₂ on standing crop biomass and productivity than had been found in systems decoupled from natural resource supply by either fertilizing, disturbing or wide spacing. Altogether, these data warn against overstating beneficial effects of a CO₂-rich world for plant growth, based on inappropriate experimental conditions for such projections or unconstrained models, in essence

based on photosynthesis. I have not presented any mean responses as became popular in such reviews, because any such mean would simply reflect the mix of data used. It is important to keep in mind that any growth stimulation would enhance forest dynamics and would translate into greater abundance of fast-growing taxa, with likely negative effects on overall carbon storage (Körner, 2004). Disregarding such forest dynamics effects, a global upper limit of net ecosystem C fixation resulting from elevated CO₂ was considered to be 10% of the projected anthropogenic CO₂ release by 2050 (Hamilton *et al.*, 2002). Even agricultural yield predictions for a *c.* 600 ppm CO₂ world have come down dramatically (to *c.* 10%), after experimental approaches adopted the relevant scales (Kimball *et al.*, 2002; Schimel, 2006). Such trials are, unfortunately, missing for the major natural forest biomes of the globe, but are urgently needed in light of the rapid alteration of the globe's carbon diet and its effects on biodiversity (Körner *et al.*, 2007). This science definitively has to move beyond primarily looking for missing carbon.

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