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

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Abstract (169 words)

In this review I am drawing attention to some constraints and biases in CO2 enrichment experiments and the analysis of literature data. Conclusions drawn from experimental works differ when the data are grouped in a way, so 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 to separate three test conditions (I) uncoupled systems (plants not depending in a natural nutrient cycle), (II) expanding systems, in which plants are given ample space and time to explore otherwise limited resources, and (III) fully coupled, i.e. steady state systems in which the natural nutrient cycling governs growth. Data for 10 type III experiments yields 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 rapidly decline with time. Plant-soil coupling (soil conditions) deserves far greater attention than the plant-atmosphere coupling (CO_2 enrichment technology).

I. A traditionally scarce resource becomes abundant

The effect of elevated CO_2 on plants has been the topic of several thousand scientific articles and approximately 120 reviews, ca. 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 (1) land transformation and the associated losses of soils, habitats for wild organisms, and the loss of and invasion by organismic taxa, and (2) the chemical composition of the atmosphere, with increasing concentrations of compounds such as CO_2, CH_4 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, CO_2 has been the basic resource for life for as long as aerobic photosynthesis exists, possibly 2.8 billion years (Tolbert, 1994), hence its sudden and rapid increase plays an exceptional role.

Over long geological periods CO_2 was overabundant. It dropped rapidly to a few percent 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 CO_2 depletion occurred during the Devonian-Carboniferous explosion of terrestrial plant life, which ended around 300 million years ago, when concentrations had fallen to

close to current concentrations, 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 years ago, CO2 concentrations became, and since then, stayed so low, that the C4 pathway of photosynthesis became evolutionary advantatious, and had 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). For the last ca. 20 million years, terrestrial plant evolution was co-driven by the optimization of the use of its ever scarce 'staple food' CO2. Most species which are dominating the current biosphere, evolved under CO2 concentrations of around 240 ppm according to ice core data for the last 650.000 years (Fig. 1). The current anthropogenic rate of atmospheric CO2 enrichment thus comes as a rather novel experience to modern plant life and the current ca. 380 ppm exceed anything plants most likely 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 years or 180 tree generations ago, when the CO2 concentration was around 180 ppm: the currently existing ca. 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 to 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 had been reviewed previously and at least 15 statistical treatments such as meta-analysis had been offered (Tab. 1), my main emphasis will be to discuss the meaning of the emerging response patterns in the context of how the data were obtained.

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 (e.g. 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, 2006). Temperature effects may come in via water relations as will be discussed later.

Tab. 1

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 ca. 80% of terrestrial productivity and the build up of more than 95% of the world's biomass C-pool of ca. 650 billion tons (Lloyd & Farquhar, 1994; Roy *et al.*, 2001), saturates when CO2 concentration approaches ca. 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 levels, 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 Tab. 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 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 CO2 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 (e.g. Nowak *et al.*, 2004; Ainsworth & Long, 2005; Zotz *et al.*, 2005).

Fig. 1

III. The fate of extra carbon

No doubt, more carbon is entering plants when leaves are exposed to elevated CO2. 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 demand. The demand by microbial partners, mycorrhizae 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 straight-forward mechanistic linkage between the rate of photosynthesis and the amount of carbon recovered in each of these compartment (Luo *et al.*, 1997). Crop physiologists were among the first to note with surprise the wide spread mismatch between photosynthetic capacity of leaves and crop biomass production (Wardlaw, 1990). Some high yielding cultivars exhibit less photosynthetic capacity than their wild ancestors.

The discrepancy between the almost uniform stimulation of leaf photosynthetic rates in proportion to a rise in CO2 concentration and rather variable growth responses, from zero to massively positive effects, had puzzled researchers for as long as this research goes on, and the puzzle has not been resolved (e.g. Novak *et al.*, 2004) and approaches at its understanding are largely advancing 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, hence the diagram inserted in Fig. 1 is not a reliable exclusive 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 co-determine where carbon assimilates will go and stay for a while (the global mean residence of carbon in biomass is 10.4 years; 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 would be included, and the whole scheme is under permanent adjustment as plants develop.

Fig. 2

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 centerpiece of any trustworthy analysis. Below 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 this might be with the

often-scarce information provided. In methods sections, atmospheric conditions commonly cover more than 10 times the printing space of below ground conditions, and 'exhaustive' statements like 'grown on the university campus' 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 greenhouse horticulture (Wittwer, 1984; see Bornemann, 1930 for one of the earliest accounts). Although, 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 non-carbon 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 aging 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 years, as had 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 determined growth or plants which 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 levels 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 (e.g. 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 average 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 or even larger responses than herbaceous plants. Because such young trees contrast non-woody plants in that they can accumulate signals over more than a few months season, 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, i.e. conditions as they mostly occur in the field, in wild plants in particular, but these conditions must first be defined in a simple as possible way. 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. estuarins), plant re-growth immediately after fire or after coppicing, or plants grown in fresh forest gaps. In large, this category includes conditions where plant growth is not tightly coupled to/or depending on a microbial rhizosphere food web, but 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 fully been explored, i.e. 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 (*sensu* Ingestad, 1982) beccomming 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 LAI reach a steady state, i.e. do not increase from year to year.

Obviously there are no sharp boundaries between these three categories. While type I and III are relatively easy to define, type II conditions might be overlooked, because they describe conditions, where a higher than sustainable supply with mineral nutrients or light comes into play indirectly, through so far insufficient exploitation of these resources per unit land area, either through low density or young age (size) of plants, compared to the carrying capacity of the land. Other co-determinants 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 far 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 type II and type III, i.e. when plants passed through type II conditions under 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 wetland 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), i.e. a fertile system prevented from arriving at steady state (Wittig *et al.*, 2005). (c) The Swiss treeline 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, the first a type I situation.

Compared to the influences of these growth conditions, the influence of the techniques of CO2 enrichment (e.g. greenhouse; open top chambers, OTCs; free air CO2 enrichment, FACE) appear almost negligible, but had 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 do quantitatively, this is largely because these CO2 enrichment methods are heavily confounded with the type of growth conditions. Greenhouse experiments are mostly done with young plants in fertile substrates (type I), open top chamber 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 had been applied in greenhouses 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 was in large driven by technological considerations which account for comparatively minor influences on microclimate,

rather than for the key subterranean co-variables, which determine plant growth responses to elevated CO2, as had been stressed in nearly all reviews of the subject (Tab. 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 to 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 had overshadowed the needed soil debate. Well designed open top chambers, the operation of which costs a few percent of a FACE operation, had 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 (e.g. Dijkstra *et al.*, 2002; Morgan *et al.*, 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, totally depend on a microbial partnership, which is an integral part of their normal functioning (e.g. Högberg & Högberg, 2002; Högberg *et al.*, 2002; Read *et al.*, 2004; see also Tab. 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) had stressed the CO2 x microbial linkage 20 years 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 & Baldocchi, 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 had 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 thus, may facilitate high absolute growth responses to CO_2 enrichment, provided other resources permit. However, elevated CO_2 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 CO_2 is permitted to influence soil moisture through reduced transpiration under otherwise unaltered atmospheric conditions, CO_2 enrichment may in fact mimic effects of better water and nutrient supply (Volk *et al.*, 2000). For biomass responses to elevated CO_2 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 which 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.*, 2006). Water savings can almost fully explain relative biomass responses of grassland to elevated CO_2, with no additional photosynthesis driven signal needed to explain the observed growth responses (Volk *et al.*, 2000; Bunce, 2004; Morgan *et al.*, 2004; Tab. 2a). This also explains why, counter expectation, C4 plants had been found to profit from CO_2 enrichment (Samarakoon & Gifford, 1996; Owensby *et al.*, 1997). Separating such water signals from photosynthesis signals seems imperative for a conclusive interpretation of CO_2 enrichment trials.

V. Plant CO2 responses as a function of time

Intentionally, the above considerations were 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, hence there is a significant leeway for interpretation, and timing of census plays a significant role for 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 had been documented for young trees in several open top chamber experiments (e.g. 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 had 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 even been 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. 3c 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. 3c represents a phase shift in development. Whether a 'pure' 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 selected in Fig. 3c, 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).

Fig. 3

When perennial plants such as trees receive a CO2 treatment after they have passed into the steady state stage of growth, 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 (Tab. 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 3b 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 3c), but mathematically, this depends on whether one uses total biomass or the increment per year only. Scenario 3c was seen in *Quercus ilex* grown around natural CO2 springs for 25 years after last coppicing (Hättenschwiler *et al.*, 1997), and in Florida scrub oak (B. Hungate, pers. comm.) following the initial post-fire stimulation (Dijkstra *et al.*, 2002). After long enough time, it becomes impossible to separate the solid line response in 3c from 3d.

CO2 effects on plant communities which have already established close to steady state fine root mass and leaf area index (canopy closure) before the test commenced, cannot propagate previous CO2-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 CO2 concentration. Unfortunately, in the case of forests and in view of tree generation times, we have little alternative to an experimental step increase in CO2 concentration, because any practical ramping would still be far steeper than the actual rise in the atmosphere of 1.5 to 2 ppm CO2 per year. Hence, CO2 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 CO2. 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 co-variant analysis or standardization by growth prior to 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 CO2 enrichment experiments (referred to above), this issue had not yet been widely discussed.

Fig. 4

VI. Plant CO2 responses per unit land area, a matter of definition

Most of the above considerations focused on growth of individual plants, based on raw data (biomass), simple to obtain and straight forward to analyse. A next step is accounting for productivity per unit land area, using a suite of approaches, which require a lot of expert skills and usually remain mysterious to non-expert 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 so. There may be little change in biomass stores (e.g. forest growth in the common sense) but substantial 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 (ca. 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 also cannot be measured, but is commonly estimated via photosynthesis models. For NEP see below.

It makes in deed 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 had in fact disappeared, 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 the size of which was never biomass, but had been recycled instantaneously to the atmosphere. While GPP estimations are more an academic exercise in this context, biomass and NPP can serve different purposes and it depends on the question one aims at answering which way of expressing CO_2 responses is more useful. Quite often the two are either confused or it is taken as granted that readers would 'prefer' NPP, hence it is implied that NPP responses to elevated CO_2 represent the more desirable quantity to be known.

This seems like narrowing the scope of biological CO_2 research to one out of several aspects, like there are: (1) plant performance, i.e. plant fitness and plant life cycle responses to the new resource supply, with implications for biodiversity and organismic interactions (e.g. herbivory, symbiosis), (2) to understand plant growth and biomass accretion (yield, biomass C-stores), and (3) 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 CO_2 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 CO_2 response or not. For instance, four FACE experiments with trees (two steady state, two rapidly expanding) arrived at ca. 20% increase in productivity (NPP), but there is no difference in above ground standing crop biomass in the Oak Ridge FACE compared to controls (Norby *et al.*, 2004, 2005) and the other three differ widely in actual biomass increment. The GPP of one, a young poplar stand, reached +250 % in the first year of CO_2 enrichment alone (Wittig *et al.*, 2005). GBP of the Basel forest FACE may be in the order of +50% (based on canopy photosynthesis data by Zotz et al. 2005),

but the actual change in biomass increment is close to zero. 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 CO_2 (e.g. isopren emission or losses as dissolved organic carbon, DOC), net CO_2 fluxes can be measured with sufficient accuracy using modern meteorological techniques which account for net vertical eddy flux and <1 ppm resolution gas concentrations. The problem is, that the release of large quantities of CO_2 in FACE experiments interfers 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 (e.g. VanKessel *et al.*, 2000; Lichter *et al.*, 2005), or by balancing estimates of NPP with estimates of respiratory fluxes (e.g. Schäfer *et al.*, 2003; DeLucia *et al.*, 2005), which incurs very large error terms which 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, the net carbon balance of soils is not. The current signal for soil carbon for a 35 % departure from pre-industrial atmospheric CO_2 concentration is in the order of 1-1.5 permille per year of mean organic C content of soils, *if* all globally 'missing carbon' were exclusively sequestered to soils. So, it is near to impossible to assess realistic changes in humus carbon stores in CO_2 enrichment experiments by mass balance calculations (Hungate *et al.*, 1996).

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

Since trees store close to 90 % of global biomass carbon, it is worth asking how CO_2 enrichment could enhance this C-pool and how experiments can contribute to this question, i.e. how a change in growth rate could translate into a bigger carbon pool per unit land area. As mentioned above, it matters whether CO_2 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 moderate 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 in 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', 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

Should elevated CO2 stimulate tree growth, trees would commonly pass through these curves faster, i.e. reach the plateau earlier in time, irrespective of whether the stimulation was restricted to the initial phase or continued life-long (Fig. 3, see discussion in 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, i.e. 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, counter still widespread belief, growth rate and biomass storage are not, or not positively correlated at landscape scale (Fig. 5). Quite often, and depending on growth stage, they are negatively correlated. When growth rate is tripled as in the right part of Fig. 5, but trees are harvested at equal size (biomass), the mean pool size over time remains unchanged. When growth rate is further doubled, but 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), but the carbon pool size is actually diminished. So growth or yield should never be confused with carbon storage, very similar to economy, where cash flow (here growth rate, carbon cycle) should not be confused with capital (here biomass-C stores). When a stimulation of tree growth by elevated CO2 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 faster reach the high storage age, a phenomenon that had been called 'buying time' (in terms of greenhouse effect mitigation). Such a transitory greater C-pools would only exist to the extent that trees are not harvested or senescing earlier. In fact, if such acceleration would occur right now, 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 at landscape scale is an issue of tree demography and not a question of growth rate. CO2 enrichment experiments do not have the power to predict future tree demography, hence are inherently unsuitable to assess trends in biomass carbon stocking in a CO2 rich world. However, they are suitable to study a large number of key plant responses to elevated CO2, 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 belief growth or NPP are synonyms of carbon storage. This is how much of the research in this field had been translated to the public media, an arena that deserves more careful use of jargon on the scientists' side.

VIII. Biomass responses to elevated CO2 in steady state and expanding systems

For all the above reasons, the following account will be restricted to biomass responses. Because CO2-effects under type I and II conditions had been reviewed extensively before (Tab. 1), the main emphasis of this account will be on responses under type III growth conditions. This restricts the analysis to 10 grassland and 3 forest studies out of hundreds of studies world wide, but never the less, the results of these studies should come closest to what might actually happen to the vast majority of ecosystems outside agriculture and forest nurseries (Tab.2). So the criteria by which works were selected

here are: steady state canopy and fine root development, and natural nutrient cycle (no fertilizer added). For comparative purposes 11 type II systems with young trees are presented in Tab 2c. These were selected by naturalness of soil conditions, broad coverage of biomes, duration and availability of comparable of data. In the following I will briefly summarize and comment the main findings of each example as listed in Tab. 2, and then offer a personal resumé.

Tab 2

Steady state grassland systems (Tab. 2a)

Kansas: No response in wet years, significant gain in dry years, largely due to the responses of Cyperaceae and forbs. There was clearly no disadvantage of C4 grasses, most likely, because they profited similarly from soil moisture savings than C3 taxa.

Montana: The mean +40 % response in biomass production was due to one C3 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 due to Cyperaceae. The effect was almost completely explained by soil moisture effects of elevated CO_2.

Swiss alpine: Clearly no response (n=12) irrespective of season or nutrient addition (n=4). 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 at a surprise, that nutrient addition, which doubled biomass, did not facilitate a CO_2 effect over four years.

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.

Nevada: There was a smaller CO2 effect on a native, but a massive effect on an exotic *Bromus* (x2.3) due to the combination of density and individual growth (+50%) responses; forbs were stimulated by +40 %. Shrubs: there was no response in dry years but a massive effect in an exceptionally wet year (shoots extension ca. x2). Root responses to CO2 were negative (less roots). The system operates far from complete ground cover.

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 5 legume species, *Onobrychis crista-galli*), 3 split plots = 6 units. Without *Onobrychis*, which is the most mesic element in this system, the CO2 effect was zero.

Summary for steady state grassland: Of the 7 natural steady state grassland systems, 3 are from a temperate summer-dry climate, 3 are Mediterranean/semiarid grass-shrublands, 1 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 more mesic nature. In no case were legumes as a group positively, and C4 grasses as a group negatively affected (no change in the C3:C4 ratio had been found around geological CO2 vents in S-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 CO2 are strongly affected by CO2 induced water savings (Morgan *et al.*, 2004). Whether such soil moisture effects and the associated biodiversity effects will occur in the future, will depend on concurrent climatic change. A 'pure' (C-driven) CO2 effect seems rare/small in these late successional systems. Once moisture effects are accounted for, the CO2 effect almost disappears hence could have been simulated with a watering treatment (Volk *et al.*, 2000). The consistently higher responsiveness of mesic taxa (which drive the overall system responses) seems to reflect the moisture savings.

Steady state tree stands (Tab 2b. Fig. 4)

Duke: Results for the (n=1) pilot project and the (n=3) replicated project 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 years. In 1999-2000 the 4th and 5th year, the combined effect (n=4) was ca. +18%, but this was due to a single treatment/control pair, which showed a response 2-8 times as high (ca. 41%) as the other 3 plots (ca. 5-17 %, Schäfer *et al.*, 2003). Without this plot-pair, the effect is down to ca. +10% in 2000. The stimulation is due to 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, peak season fine root biomass remained stimulated, and associated below ground metabolic activity is enhanced. So 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 unit are not plots (n=1) but individual trees (n=10, each covering 30-100 m^2 of canopy) belonging to 4 different species. As in the other experiments, there was a strong initial stimulation in tree basal area, but in one of the 4 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 pre-treatment 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 CO_2 after canopy closure had been reached, revealed a strong initial stimulation of growth or NPP, followed by a subsequent decline. LAI remained unaffected and photosynthethic capacity showed no downward adjustment. At Oak Ridge the remaining signal is annual fine root production, at Duke stems are the prime responsive unit, but the means strongly depend on one particularly stimulated CO_2 plot. Duke

trees also started to reproduce earlier, hence development was accelerated. Trees in the Basel FACE had 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 the expected or even no 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 (Tab. 2c)

Swiss tropical: Because of the very rapid growth at daytime temperatures close to 30 °C, high humidity and fertility, this complex 15 species model community more than doubled its height and biomass (corresponding to a 2800 g m-2 a-1 increase in biomass) in only 3 month (from LAI 3.4 to steady state 6.8 in 2 months). There was no significant effect of CO2 on aboveground biomass or LAI (stems +7%), but root mass (ca. +50%) and soil metabolism (doubling) were strongly enhanced while the canopy approached and reached closure.

Italian CO2 spring: At two different CO2 vents and close-by reference stands in Toscany, *Quercus ilex* shows a significant stimulation by CO2 enrichment in the years following coppicing. After ca. 25 years the relative difference in radial annual stem increment is zero, but the stems, which re-sprouted under high CO2, retained a greater diameter, which corresponds to a 3-year advancement in development. Most of the effect after the initial stimulation comes from prior effects on accelerated canopy development. Leaf area per branch unit was reduced.

Florida scrub oak: Re-growth after burning is strongly stimulated by elevated CO2. Not yet at steady state (max. 2.3), LAI is always higher at elevated CO2, but the stem diameter response to CO2 declined rapidly, and in later years, the compound interest effect from prior acceleration of canopy development alone, would be greater than needed to explain actual biomass responses. There is clear evidence for a slowing of the N-cycle with time.

Tennessee oak: CO2 responses in year one were strong. Later responses were exhaustively explained by compound interest effects, i.e. the differences in annual biomass increment at unchanged photosynthetic capacity reflected the difference in leaf area set in the previous year. The biomass after 4 years in elevated CO2 was more than double that in ambient air, because of this initial acceleration in development.

Wisconsin aspen/birch/maple: After 7 years, the combined diameter and height growth effects of elevated CO2 accumulated to 25, 45 and 60 % in aspen alone or in mixtures with birch or sugar maple. Given that each of year 2 and 3 responses arrived already at +22 and +28 % for aspen, the annual stimulation had been drastically reduced in later years and became less than what would be expected from a compound interest effect on the third year advance of CO2 enriched stands alone.

Oregon lowland douglas fir: Elevated CO2 did not affect biomass production or allocation and LAI. There was no CO2 x temperature interaction, i.e. simulated warming did not facilitate a CO2 effect on biomass, but there were some effects on leaf chemistry.

Swiss lowland spruce/beech: This is the only CO2 experiment that was replicated over two different soil types (Fig. 6). The CO2 effect on growth was determined by soils, beech was negatively affected by CO2 on acidic soil, but profited on calcareous soil. Spruce profited on both soil types. CO2 stimulations of growth occurred during year 1 and 2, but disappeared during year 3 and 4. The final biomass was not affected on acidic soil, but due to the initial stimulation, was higher on calcareous soil. LAI was not affected by CO2 under natural soil fertility.

Swiss montane spruce: There was no growth response to elevated CO2 at any time (similar to the Oregon experiment), except if nutrients were added. In fact, on un-amended natural soil, the vigor of trees declined under a 3 year exposure to elevated CO2 (reduced LAI). Soil C-metabolism was strongly enhanced, however.

Sweden boreal spruce: After four years of growth, there was no overall CO2 effect on stem growth irrespective of whether nutrients were added or not. However, there was a significant stimulation in year two in the unfertilized group (n=3), which lines up with other initial effects of CO2 enrichment. Some wood properties changed however.

Swiss treeline: After four years, there was no CO2 effect on pine, but the co-occurring larch shows a continuous stimulation. These trees are standing isolated in a matrix of dense dwarf shrubs, hence canopies can freely expand, but there is below ground competition. In *Larix*, compound interest effects of initial canopy enlargement seem to be propagating, so trees continue to expand their crowns faster.

Summary for expanding tree stands: In these 10 examples, selected for their close to natural soil conditions, young trees were permitted to approach (from juvenile, seedling or cutting stage) a closed canopy community. 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 studies have found no growth stimulation by elevated CO2, when no extra nutrients were provided (e.g. Barton & Jarvis, 1999; Winter *et al.*, 2000; Maroco *et al.*, 2002). In the other cases, true CO2 responses were restricted to the first or first few years, with compound interest effects propagating these initial differences in canopy development. The final difference thus depends on the years to canopy closure and time of harvest. The cumulative biomass effect after 3-7 years 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. 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).

IX. Conclusions

In this review I tried to highlight major co-determinants of plant CO2-responses, which need to be accounted for, should the resultant trends not just reflect the abundance of a certain type of studies (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 as had previously emerged from not separating expanding versus steady state, fertilized versus unfertilized or young versus 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 semi-natural grasslands, which depend more on shallow soil moisture, CO2 effects are strongly tied to water savings (Morgan *et al.*, 2004), so the 'pure' CO2 effect becomes overshadowed and responses cannot directly be 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 to trees whose crowns had formed close canopies before the 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 (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 had steady state LAI been increased under elevated CO2, 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 had been found accelerated, when tree canopies experienced elevated CO2 (e.g. Körner & Arnone 1992; King *et al.*, 2004). There is consensus in the literature that the nutrient cycle sets the ultimate limit to a carbon driven, long term stimulation of plant production (e.g. Finzi *et al.*, 2002, Hungate et al. 2006). Soil conditions and plant species exert overarching influence on experimental results (Fig. 6) and thus deserve more attention in experimental design. For affecting 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 time scales needed (Lichter *et al.*, 2005).

Fig. 6

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 at 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 had not presented any mean responses as became popular in such reviews, because any such mean would simply reflect the mix of data used. A best guess may be that the upper limit of a long-term steady biomass response is below +10 %, with steady state effects close to zero being most likely under natural conditions. The biosphere may in fact be carbon saturated already at current CO2 concentrations (Körner, 2003b). 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. Disregarding such forest dynamics effects, a global upper limit of net ecosystem C-fixation due to 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 double CO2 world have come down dramatically (to ca. 10%), after experimental approaches adopted the

relevant scales (Kimball *et al.*, 2002). 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 globes carbon diet and its effects on biodiversity (Körner *et al.*, 2006). This science definitively has to move beyond primarily looking for missing carbon.

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Nowak Tansley review als 10 einfügen, alles um 1 verschieben das >10 ist

Tab.1 A selection of reviews and conceptual papers on plant and ecosystem responses to elevated CO2 (s for statistical assessments such as meta-analysis). The list also includes synthesis articles of long-term studies or original articles, which include exceptional literature accounts. Since specific subjects are often also treated in general reviews, the latter are keyed these subjects, if the emphasis was special.

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

 1Lemon 1983, 2Long & Hutchin 1991, 3Woodward *et al.* 1991, 4Gifford 1992, 5Poorter 1993s, 6Amthor 1995, 7Ward & Strain 1999, 8Körner 2000, 9Ainsworth & Long 2005s, 10Nowak *et al.* 2004, 11Körner *et al.* 2006, 12Wittwer 1984, 13Acock & Allen 1985, 14Ainsworth *et al.* 2002s, 15Kimball *et al.* 2002, 16Kim *et al.* 2003, 17Polley *et al.* 1997, 18Körner 2002, 19Niklaus & Körner 2004, 20Lüscher *et al.* 2004, 21Morgan *et al.* 2004, 22Eamus & Jarvis 1989, 23Norby 1996, 24Jarvis 1998, 25Körner 1998, 26 Saxe *et al.* 1998, 27Ceulemans *et al.* 1999, 28Norby *et al.* 1999, 29Gielen & Ceulemans 2001, 30Kerstiens 2001, 31Beedlow *et al.* 2004, 32Arp 1991, 33Long & Drake 1992, 34Preiss 1994, 35Berry *et al.* 1994, 36Curtis 1996s, 37Stitt & Krapp 1999, 38Peterson *et al.* 1999s, 39Medlyn *et al.*

1999s, 40Ghannoum *et al.* 2000, 41Poorter *et al.* 1992, 42Drake *et al.* 1999, 43Eamus 1991, 44Tyree & Alexander 1993, 45Hsiao & Jackson 1999, 46Wand *et al.* 1999s, 47Medlyn *et al.* 2001s, 48Poorter & Perez-Soba 2001, 49Kergoat *et al.* 2002, 50Bunce 2004, 51McGuire & Melillo 1995, 52Cotrufo *et al.* 1998s, 53Hungate 1999, 54Yin 2002, 55O'Neill 1994, 56Diaz 1996, 57Paterson *et al.* 1997, 58Tate & Ross.1997, 59Arnone *et al.* 2000, 60Treseder & Allen 2000, 61Zak *et al.* 2000, 62Norby *et al.* 2001s, 63Pendall *et al.* 2004, 64King *et al.* 2004, 65Rawson 1992, 66Cannell & Thornley 1998, 67Kirschbaum 2004, 68Zvereva & Kozlov 2006, 69Lincoln *et al.* 1993, 70Porter *et al.* 1997, 71Bazzaz & McConnaughay 1992, 72Possingham 1993, 73Diaz 1995, 74Körner & Bazzaz 1996, 75Niklaus *et al.* 2001, 76Navas *et al.* 2002, 77Poorter & Navas 2003, 78Reich *et al.* 2004, 79Reekie 1996, 80Ceulemans 1997, 81Jablonski *et al.* 2002, 82Loehle 1995, 83Körner 1995, 84Hungate *et al.* 1996, 85Luo *et al.* 1997, 86Sage & Cowling 1999, 87Körner 2003

Tab. 2. Grassland and forest test systems which have reached a steady state growth before (a, b; type III systems) or approached it during CO2 enrichment (c, i.e. expanding systems of type II). The number of species and years of operation refer to the references mentioned. Tree model systems were included preferentially when they were sustained into steady state LAI and were using un-amended natural forest soil. See text for results.

Name of site (no. species/dom.)	Type of vegetation	Duration (years)	Replic. (n)	Reference examples
(a) Steady state grassland systems (type III) *				
Kansas (>12/3)	tall grass prairie	8	3	Owensby *et al.* 1999
Montana (35/3)	short grass prairie	5	3	Morgan *et al.* 2004
Swiss low (25/3)	calcareous grassl.	6	8	Niklaus & Körner 2004
Swiss alpine (10/2)	alpine grassland	4	12/4	Körner *et al.* 1997
California (-/4)	Mediterr. annual	3	8	Shaw *et al.* 2002
Nevada (>12/4)	desert annual/shrub	4	3	Smith *et al.* 2004/Nowak *et al.* 2004
Negev (25/3)	semiarid annual	1	3/6	Grünzweig & Körner 2001
(b) Steady state forest systems (type III) **				
Duke (1+)	conifer plantation	4 (10)	1/3/4	Oren *et al.* 2001, Schäfer *et al.* 2003
Oak Ridge (1)	deciduous plantation	6 (9)	2	Norby *et al.* 2004
Basel (4)	mixed deciduous forest	4 (6)	1	Körner *et al.* 2005
(c) Expanding young tree stands (type II systems) ***				
Swiss tropical	15 species	0.3	2	Körner & Arnone 1992
Italian CO2 springs	Quercus ilex	30	2	Hättenschwiler *et al.* 1997
Florida	Quercus sp.	7(10)	8	Dijkstra *et al.* 2002, Hungate p.c.
Tennessee	Quercus alba	4	4	Norby *et al.* 1995
Wisconsin	Populus tremuloides with Betula and Acer	7(9)	3	King *et al.* 2005
Orgeon	Pseudotsuga menziesii	4	2/3	Olszyk *et al.* 2003
Sweden	Picea abies	4	3/6	Kostiainen *et al.* 2004

Swiss lowland	Picea abies and Fagus sylvatica	4	4	Spinnler *et al.* 2002
Swiss montane	Picea abies	3	6	Hättenschwiler & Körner 1996
Swiss treeline	Pinus uncinata and Larix decidua	3(6)	5/10	Handa *et al.* 2005

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* The longest test series, that of a *Scirpus* estuarin system, is a category in its own, because it is in a steady state, but due to 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 very close to natural situation for this ephemeral desert vegetation.

** These are the three only test systems with closed forest canopy. Years are given for the periods for which the needed data were available (in brackets total duration by 2006)

*** All these type II test conditions started with small isolated plants, either seedlings, cuttings or re-sprouts after coppicing or burning. Examples selected preferentially reached close to steady state LAI by the time of the final harvest, although plants were still very young and the experiments closed before 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 stands had been thinned in year 3 'to optimize spacing' and the Swiss montane and Tennessee tests used 2 elevated CO_2 concentrations. Note, duration refers to season, which in the case of temperate montane, boreal or Mediterranean is 4-5 month per year, in the warm temperate zone 6-7 months and 12 month in the tropics.

Legends to Figures

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.

Fig. 2 The fate of carbon in plants. A schematic presentation of uptake, allocation and export of carbon, with examples of feedback responses. (With permission from Blackwell Publishers, from Körner, 2003a).

Fig. 3 A schematic presentation of 4 different types of CO2 responses of plants when CO2 exposure is initiated at the seedling or rooted cutting stage (type II growth conditions). (a) No CO2 effect, (b) continuous CO2 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 CO2 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 objects the law of limiting resources (except for short periods), so variants of (c) are most likely. Note, the constant difference between the two solid lines after the breakpoint in (c) results in diminishing relative responses with time.
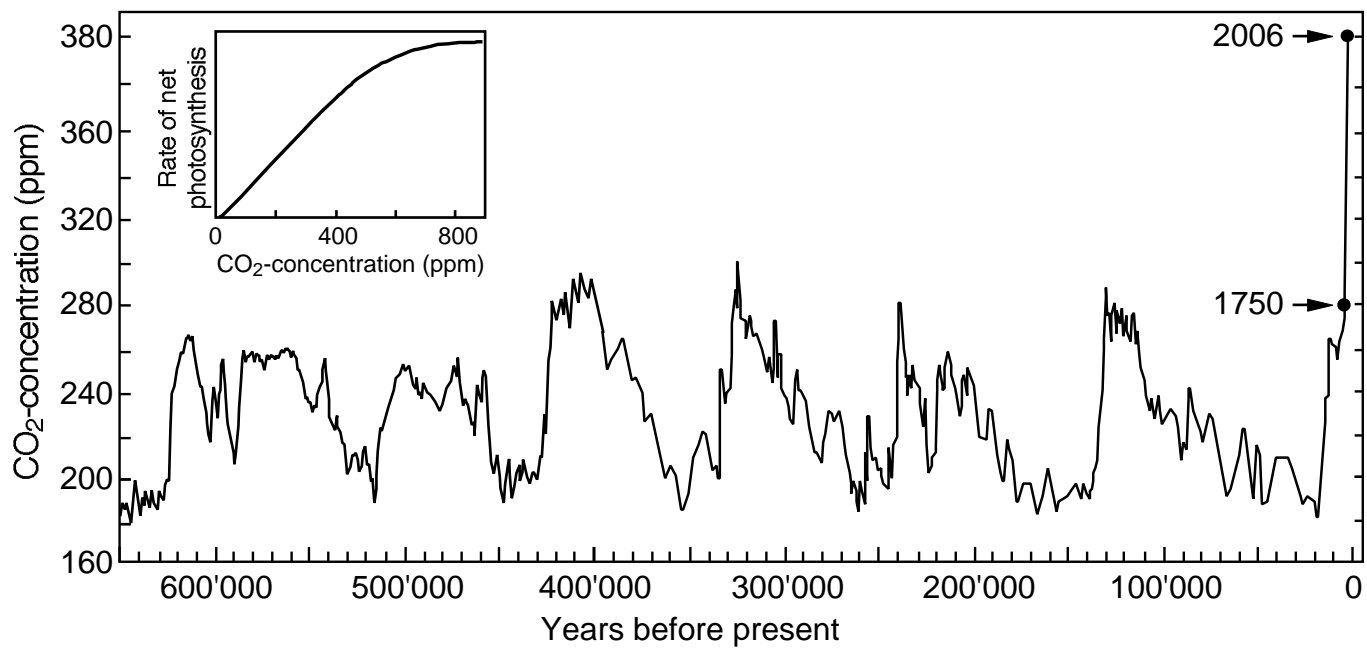
Fig. 4 Above ground growth responses of forest trees to elevated CO2 in the three existing forest-scale CO2 enrichment experiments. E/A ratios (elevated vs. ambient CO2) are either for annual tree basal area (Swiss) or above-ground biomass increment/NPP (other experiments), which does not affect the overall trend of strong initial and reduced later CO2 responses. Duke I depicts the single 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 exaggerated stimulation in year 4 for unknown reasons. The Oak Ridge data are from Norby *et al.* (2004), and the Swiss data from Körner *et al.* (2005). For the sake of clarity, data points and error bars have been omitted, and trends were smoothed by hand.

Fig. 5 Idealized growth curves of trees growing at slow (a), three and six times as fast (b and c) rates. In a and b, trees grow to equal individual mass, in c trees are harvested in accordance to economic maximum yield scenarios (rapid rotation plantation). The horizontal dashed line indicates the mean biomass storage over the whole life cycle, which is not different in a and b, but lower in c. These single tree growth curves also apply to equal aged stands. In a commercial forest landscape, all tree/stand age classes ideally would 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.

Fig. 6 A schematic, stepwise representation of the results of the only CO_2 enrichment experiment so far which employed two different native soils (on which two test species co-occur naturally) in a fully replicated (n=4) CO_2 x N treatment over four years. 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 competing spruce on calcareous soil under elevated CO_2 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 x CO_2 interaction matrix. The results underline the overarching significance of soil conditions and species identity in CO_2 research (from data in Spinnler *et al.*, 2002).
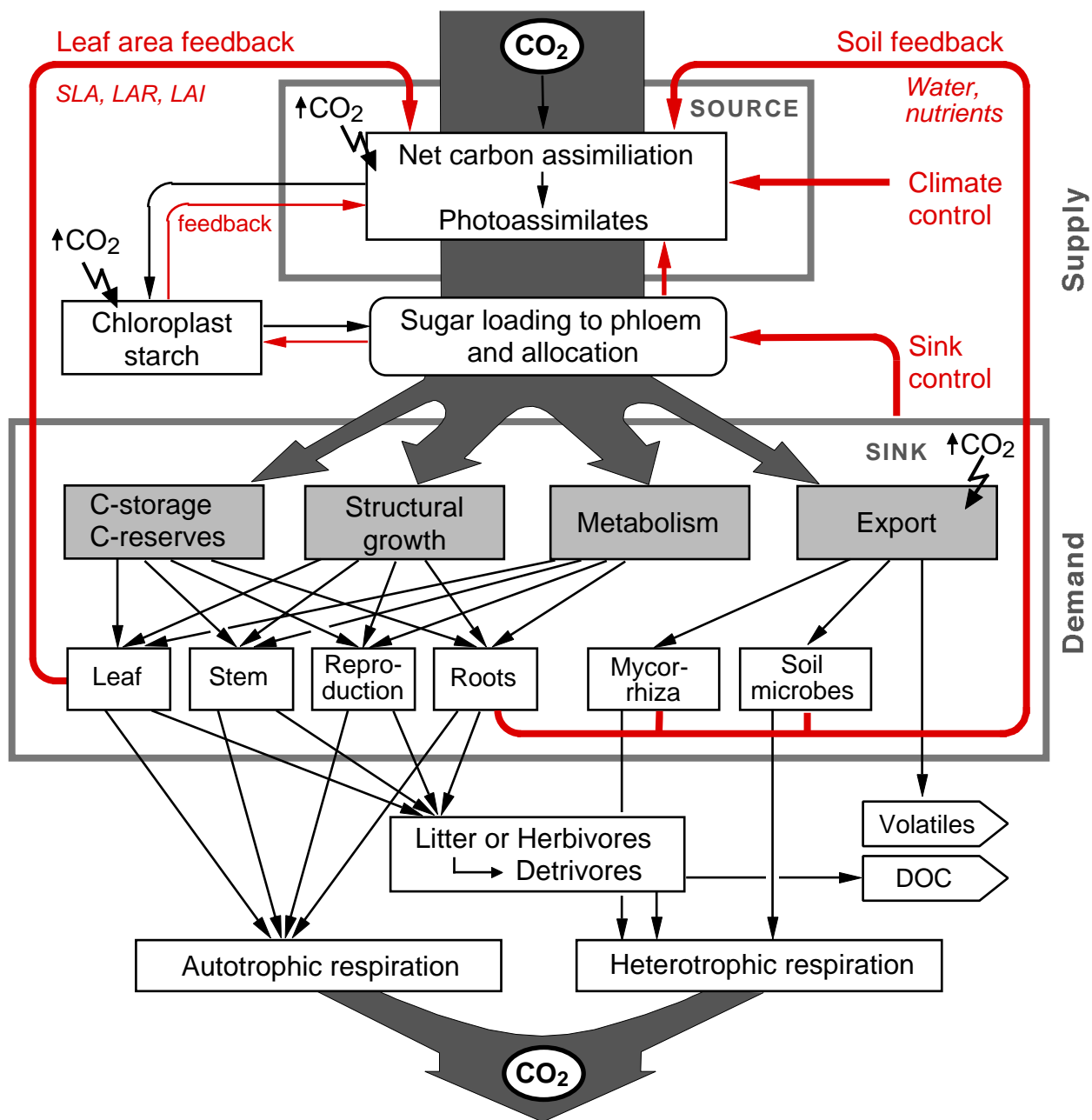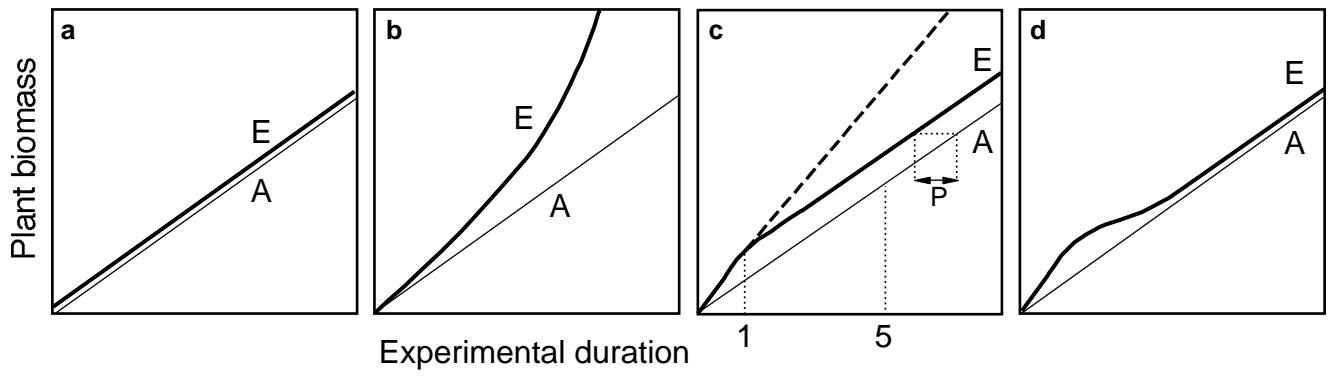
Fig 1

Fig 2

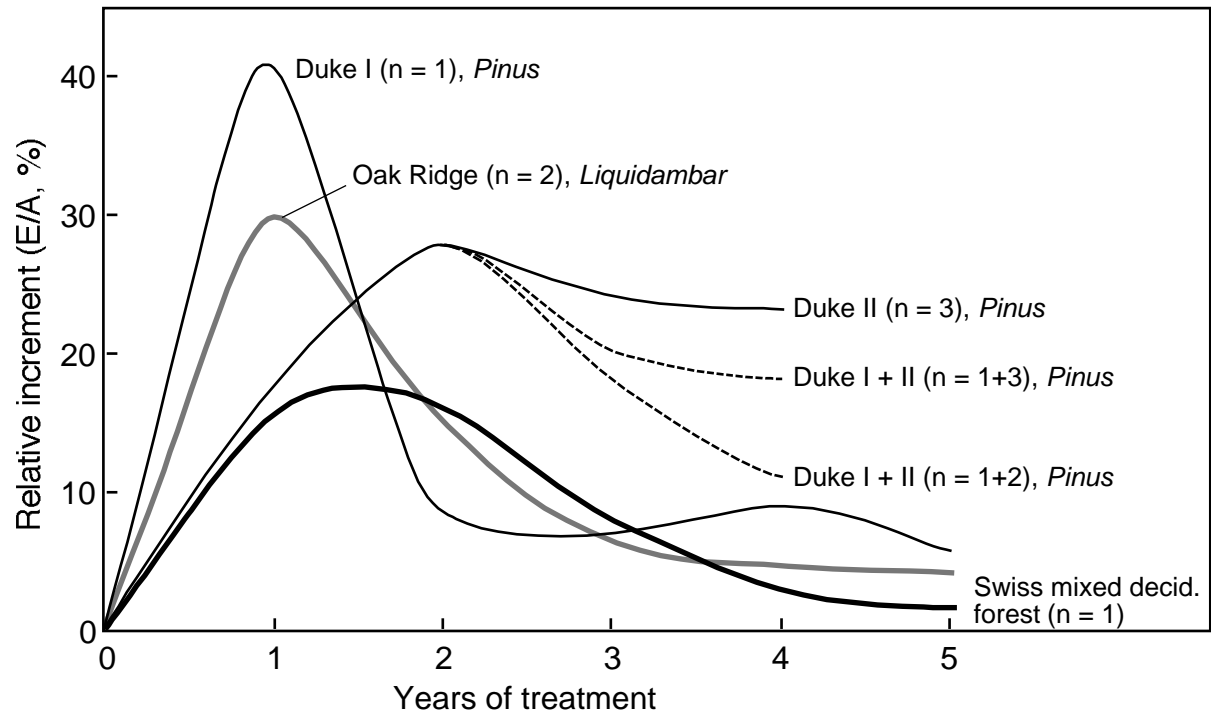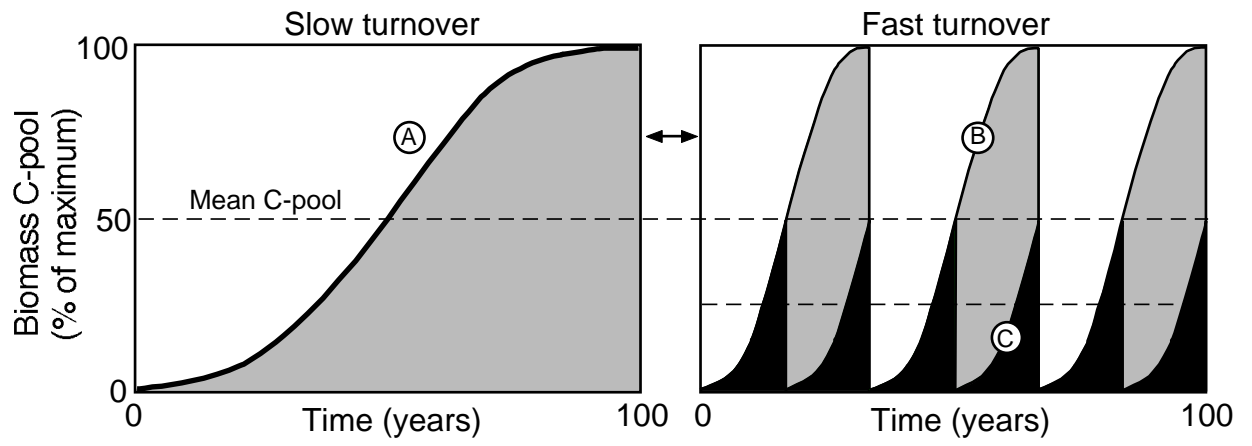# The fate of carbon in plants

Fig 3

Fig 4

Figure content labels: Relative increment (E/A, %) on y-axis (0 to 40); Years of treatment on x-axis (0 to 5). Curves labeled: Duke I (n = 1), Pinus; Oak Ridge (n = 2), Liquidambar; Duke II (n = 3), Pinus; Duke I + II (n = 1+3), Pinus; Duke I + II (n = 1+2), Pinus; Swiss mixed decid. forest (n = 1).

Fig 5

Slow turnover

Fast turnover

Biomass C-pool (% of maximum)

100

50

0

Mean C-pool

Ⓐ

Ⓑ

Ⓒ

Time (years)

0

100

0

100

Fig 6