Oecologia (2013) 171:639–651
DOI 10.1007/s00442-012-2584-5

SPECIAL TOPIC: IN HONOR OF CHRISTIAN KÖRNER

Beyond global change: lessons from 25 years of CO_2 research

Sebastian Leuzinger · Stephan Hättenschwiler

Received: 2 May 2012 / Accepted: 18 December 2012 / Published online: 10 January 2013

Abstract Over the past 25 years, countless experiments have been conducted on the impact of increased atmospheric CO_2 concentration on various plants and ecosystems. While this research was motivated to better understand and predict how rising CO_2 will affect the structure and function of ecosystems in the future, it also shed light on some general, CO_2-research independent, aspects in ecological research. Interestingly, it is these general aspects that continue to create confusion and lead to misinterpretation. Here, we focus on seven interrelated key issues including (1) the confusion between fluxes and pools, (2) the stoichiometric aspects of growth and biomass production, (3) resource allocation within organisms, (4) data scaling and the choice of a reference metric, (5) the consideration of time and timing (experimental duration, ontogenetic shifts), (6) confounding and second-order (indirect or feedback) effects, and (7) the key role of biodiversity. The principles deriving from addressing these issues relate strongly to each other. Their concurrent consideration requires experimenters and modellers to likewise maintain a broad, holistic perspective. In this synthesis, we attempt to show how appropriate consideration of these principles can greatly enhance the assessment of the validity, plausibility and generality of experimental and modelling results. We conclude that neglecting to adequately address these key issues in ecological research may lead to overestimations of measured responses and/or simplistic interpretations. Our examples mostly originate from research on plant responses to elevated atmospheric CO_2, but are also applicable to other areas of ecological research. We provide a checklist for the planning of ecological field experiments and the interpretation of their results that may help in avoiding common pitfalls.

Keywords Biodiversity · Resource allocation · Stoichiometry · Ecology · Up-scaling · Timing

Introduction

Research on the effects of elevated atmospheric CO_2 concentrations on plants and interacting organisms and ecosystems (here loosely summarised by the term 'CO_2 research') played a major role in global change ecology over the past 25 years. A vast number of original research, synthesis and review papers have been published on this topic since the late 1980s. A crude search in the Web of Science® for the keywords "elevated" and "CO_2" and "plant" yields more than 5,500 results in September 2012 with 5,300 of them published after 1987. CO_2 research exploded in the 1990s with an average of 105 papers per year in the 4 years 1991–1994 compared to only 3 papers per year during the 4-year period between 1987 and 1990.

Communicated by Russell Monson.

S. Leuzinger
School of Applied Sciences, Auckland University
of Technology, Auckland 1142, New Zealand

S. Leuzinger
Institute of Botany, University of Basel, Schönbeinstrasse 6,
4056 Basel, Switzerland

S. Leuzinger (✉)
Forest Ecology, Department of Environmental Sciences,
ETH Zurich, Universitätstrasse 16, 8092 Zurich, Switzerland
e-mail: Sebastian.Leuzinger@env.ethz.ch

S. Hättenschwiler
Centre of Evolutionary and Functional Ecology, CEFE-CNRS,
1919, Route de Mende, 34293 Montpellier, France

The counts for 2001 and 2011 yield 286 and 398 papers, respectively. Inevitably, the chosen search terms miss some relevant literature not mentioning "plant" in their title, keywords or abstract.

Many excellent reviews have synthesised this large body of literature over the years (e.g. Ceulemans and Mousseau 1994; Curtis and Wang 1998; Norby et al. 1999; Körner 2003c; Ainsworth and Long 2005; Körner 2006; Norby and Zak 2011). With this paper, we do not intend to add another review. Rather, we present some thoughts and ideas that have been stimulated by the research and teaching of Christian Körner, with whom we both had the privilege to collaborate over many years. We gathered seven items (issues, problems, topics, concepts—none of these provide an accurate umbrella term) that have often been brought up and discussed around the research led by Christian Körner. Whilst we tried to consider the relevant literature for each topic, we acknowledge that there is a (intentional) bias towards his and his colleague's work, and sometimes other examples could have been used to illustrate our points. Because we think that the raised issues are all relevant for general ecology, the following seven topics are introduced quite broadly, followed by examples from CO_2 research, and mostly end in a more generally valid conclusion. The summary table given at the end reflects this and is not specific to CO_2 research.

We dedicate this paper to Christian to acknowledge the fundamental influence he has had and continues to exert on CO_2 research in particular and the global ecological research community in general, but also on our personal scientific development and that of many others.

Fluxes are not pools

Systems consisting of pools that are interconnected by fluxes are common in nature (e.g. the global cycles of chemical elements and water) as well as in the human-made world (e.g. the global monetary system, traffic systems). Confounding fluxes with pools within the global carbon cycle is deeply rooted both in the non-scientific as well as in the scientific world, and this has caused a lot of misconception among scientists and policymakers alike (Körner 2009a; Körner et al. 2007). Although the distinction is quite simple (a person with a high income does not necessarily have a lot of money when the expenses compensate the income, and a person with no or a small income may be very wealthy because of accumulated riches in the past), large carbon (C) fluxes are mostly implicitly and sometimes explicitly interpreted as leading to large changes in the respective pools. A recent study published in *Nature* opens with the statement: "Nitrogen (N) limits the productivity of many ecosystems worldwide, thereby restricting the ability of terrestrial ecosystems to offset the effects of rising atmospheric CO_2 emissions naturally" (Morford et al. 2011). While the first part of the sentence clearly refers to a flux (productivity), the second refers to a pool (C sequestration), and the causal link made between the two is far from obvious. Other prominent examples include the early optimistic extrapolations from the CO_2-fertilising effect on leaf photosynthesis and biomass accumulation in expanding systems (Idso and Kimball 1993; Kimball et al. 1993). Because individual fluxes such as leaf-level net assimilation can be offset, for example, by night-time leaf-level respiration, they are of limited interest, unless (1) they are viewed in relation to the other fluxes connected to the system (i.e. the net in-or-out flux is determined), and (2) they are observed over long enough time periods and expressed per unit of time (see also "The issue of the reference metric" and "The role of time and timing" below). It is further important to appreciate the size of the fluxes relative to the pools they connect and whether fluxes are directly compensated resulting in small net fluxes. For example, although a total amount of about 4 trillion dollars (US$ 4×10^{12}) is transferred daily (matching approximately the global monetary volume), "the poor stay poor and the rich get rich" (Cohen 1988), i.e. the pools remain approximately constant despite large fluxes.

An admittedly simplified view of the global terrestrial C cycle (Chapin et al. 2009; Le Quere et al. 2009) features essentially three C pools of the same order of magnitude (the atmosphere, the soil and the vegetation pools) and four C flux pathways (gross photosynthesis, dark respiration, litter input, and soil respiration), also comparable in size (Fig. 1). The physiological sensitivity of vegetation to atmospheric CO_2 has posed some fundamental questions on how this global cycle will be affected in the future (Norby and Zak 2011), with the key interest on the long-term equilibrium among the three main pools (Fig. 1; Luo and Weng 2011). We argue that the focus of the past 25 years of CO_2 research may have suffered from (1) the unbalanced consideration of the four main fluxes mentioned above, and (2) the omnipresent, mostly implicit misinterpretation of C fluxes as C pools. For example, a systematic search of the scientific literature shows that a disproportional effort has been put into studying photosynthesis under global change (576 publications; see Fig. 1 for detailed search pattern), and only a fraction of this effort was directed to studying dark respiration (36 publications), soil respiration (112 publications) and litter decomposition (122 publications). Although this is a very rough picture of the conducted research, it suggests a strong bias. Leaf-level photosynthesis at elevated CO_2 concentrations is very well documented in situ, with little variation across plant functional types and ecosystems (mean increase of 30 % at elevated compared to ambient

CO_2 concentration; Ainsworth and Long 2005; Ainsworth and Rogers 2007). However, whether the additionally assimilated carbon leads to increased standing biomass per unit area is entirely unknown on the basis of photosynthesis data alone. Especially, C fluxes from the plant to the soil via litter decomposition, foliage leaching, rhizodeposition and transfer to mutualistic microorganisms are very poorly quantified, yet they represent key determinants for the fate and residence time of C within particular plant and soil pools (Norby and Zak 2011). Long-term eddy flux data are useful because they characterise the net C in- or outflux of an ecosystem. However, this method cannot be used to study manipulative experiments, because the treated areas are too small. Also, when up-scaling eddy flux data, it is important to consider the fact that they do not represent a typical sample of the earth's surface area (Körner 2003d). Given the considerations so far, research on the global carbon cycle should (1) investigate the key C fluxes with approximately equal priority, and (2) concentrate on the state of the long-term pools rather than quantifying short-term fluxes (e.g. using space-for-time approaches).

The stoichiometry issue

In any process of construction or build-up of non-living objects such as cars or houses, or of living organisms such as plants or microbes, an increase of a particular resource can accelerate the process only as long as other essential resources are not limiting. Examples are omnipresent (construction sites, supply-chain management, dietary needs of humans). This obvious, but often neglected, fact may provide answers to some of the most fundamental questions in ecology, such as why there is so much plant biomass on earth that is not consumed by herbivores (Polis 1999; Sherratt and Wilkinson 2010). Abundant food is only one of the required resources by herbivores, but for successful reproduction they need many more (e.g. a mate, suitable climate, space). On geological time scales, the projected doubling of atmospheric CO_2 (from ca. 1850–2050; IPCC 2007) instantaneously provides plants with a substantial increase of a key resource that was scarce for at least several hundreds of thousands of years (Petit et al. 1999). The question of how plants respond to this is of interest from a purely ecological perspective, but it is also fundamental to mankind because of the potential to compensate anthropogenic CO_2 emissions.

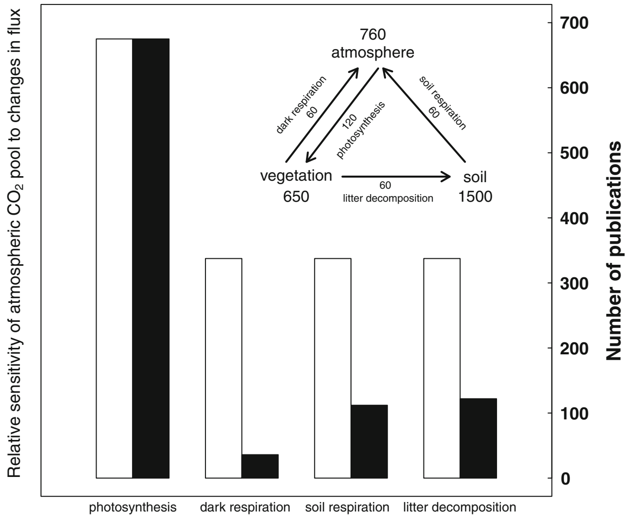

Fig. 1 A simplification of the terrestrial carbon cycle with the key pools and fluxes (*inset*, see text), and the sensitivity of the atmospheric pool to those fluxes (*white bars*, *left axis*) and the number of publications found on Web of Knowledge^{SM} combining the topics "global change" with either "photosynthesis", "dark respiration", "soil respiration", or "litter decomposition" (*filled bars*, *right axis*). Given their relative importance, the latter three are underrepresented in our current research

Some early experiments reported impressive stimulation of biomass production in response to elevated atmospheric CO_2 concentrations (Idso and Kimball 1993; Kimball et al. 1993) that had initially been interpreted as strong evidence for increased land area-based productivity and C sequestration in a future anthropogenically CO_2-enriched atmosphere. Quite typically for this first series of experiments in the late 1980s–1990s, resources other than CO_2, such as water, light (space) or nutrients, were provided abundantly. Strong CO_2 responses under horticultural conditions with non-limiting resources came without surprise (Körner 2003c) and were recognised as early as the late 1800s. Later, more complex experiments simulating conditions plants experience in their natural environment showed that a CO_2-fertilisation effect is rather the exception than the rule (e.g. Hättenschwiler and Körner 1998; Körner and Arnone 1992). Carbon is just one among many resources required by plants for their growth, reproduction and persistence, and increasing evidence indicates that growth of plants in their natural environment is not primarily limited by C (Hoch and Körner 2003; Körner 2003b; Millard et al. 2007; Würth et al. 1998).

Some of the larger-scale FACE experiments in close to natural ecosystems that have been running for about 10 years showed that N availability in particular limits plant responses to elevated CO_2 (Norby et al. 2010; Oren et al. 2001; Reich et al. 2006). This N control was described as "Progressive N Limitation" (PNL) stating that soil N availability ultimately limits plant biomass responses to elevated CO_2 (Finzi et al. 2006; Luo et al. 2004). Together with phosphorus (P), N is quantitatively and functionally the most important nutrient. Quantitatively, these two nutrients are among the six major elements that build up biomass, and functionally they are fundamental for metabolic activity, growth and development as major elements in proteins, DNA, RNA, or ATP. The key role of these elements and their balance relative to C have long been recognized and led to the development of the theory of ecological stoichiometry (Elser et al. 2000; Redfield 1958). Based on the observed constant C:N:P ratio of 106:16:1 in the biomass of marine plankton (Redfield 1958), ecological stoichiometry predicts relatively well-constrained elemental ratios in biomass (Elser et al. 2000). PNL in CO_2 experiments confirms this prediction, and shows that the conversion of higher amounts of assimilated C under elevated CO_2 into biomass depends on an equilibrated N availability.

In a CO_2-enriched atmosphere, plants may compensate for limiting N through increased N mineralisation from priming-induced soil organic matter decomposition (Drake et al. 2011) or through increased access to N in deeper soil horizons by allocating C to deeper growing roots (Iversen et al. 2011). However, higher soil N availability at elevated CO_2 does not necessarily translate into higher plant biomass production per unit land area (Körner et al. 2005; Schleppi et al. 2012), because stoichiometric constraints extend to elements other than N. More generally, we may state that any biomass response to elevated CO_2 is controlled by the stoichiometric balance of a multitude of elements required for the construction of new tissues and for an active metabolism. Apart from N, the role of frequently limiting elements such as P, or K, or some micronutrients (e.g. Mn, Fe) in plant and ecosystem responses to increasing atmospheric CO_2 were, however, rarely examined. For example, a literature search in the Web of Science® with the three search terms "elevated CO_2" and "phosphorus" and "biomass" yielded a total of 131 references, but only a minority of them (15 studies) actually tested the interactive effects of elevated CO_2 and P availability on plant biomass production. In one of the first experiments combining increased atmospheric CO_2 concentrations with P fertilisation, Stöcklin and Körner (1999) showed a particularly strong increase in biomass production of legumes exposed to a combined CO_2 and P fertilisation in grassland model communities. This result provides strong evidence for stoichiometric control on CO_2 effects, as the N_2-fixing legumes were largely independent of soil N availability and P was artificially added in surplus. In contrast, non-N_2-fixing forbs showed no biomass response to elevated CO_2 irrespective of P fertilisation, indicating that increased availability of both N and P was a prerequisite for a positive CO_2 effect on biomass production in forbs. Phosphorus should be particularly important for the understanding of plant and ecosystem responses to rising atmospheric CO_2 in tropical forests that are typically growing on highly weathered and P-deficient soils (Vitousek and Sanford 1986). Despite the critical role of humid tropical forests in global biogeochemical cycles, there has been no large-scale in situ experiment testing some important hypotheses of tropical forest responses to elevated CO_2, that have been put forward on the basis of a few small-scale seedling studies and experiments with model ecosystems (Körner 2009b). The lack of such experiments in the tropics represents a serious gap in our knowledge on the impact of rising atmospheric CO_2 on global biogeochemical cycles and their interactions governed by stoichiometric principles (Luo et al. 2011).

Ecological stoichiometry is clearly pivotal for the understanding and reasonable predictions of the effects of rising atmospheric CO_2 concentrations on NPP and C sequestration. A unit of fixed C requires a corresponding assimilation of the remaining 29 elements required by living organisms. These will not change in concert with increases in C availability. Consequently, there might be little potential for higher NPP and additional C sequestration to compensate for rising anthropogenic CO_2 based on stoichiometric considerations.

The role of an organism's resource allocation

A closely related subject to the relative abundance of different essential resources is how and where an organism invests them. An analogy from economics is the trade-off any company (the organism) is facing: should earnings be saved for hard times to come (allocation to storage) or should they be reinvested immediately in order to increase production (allocation to growth)? The strategy of a company will determine its success or failure on the market. Similarly, an organism's fitness depends to a great extent on resource allocation to different structures and functions (e.g. growth, maintenance, defence, reproduction, storage).

Resource allocation in plants is controlled by a multitude of factors including functional type and species-specific allocation patterns, ontogenetic stage of the plant, competition by neighbours, predation, resource availability, and environmental conditions (Bazzaz and Grace 1997; Poorter et al. 2012). The concept of "optimal partitioning" (Bloom et al. 1985; Gedroc et al. 1996), or, in its wider definition, also referred to as the "functional equilibrium" (Reynolds and Thornley 1982; Brouwer 1962), provides a widely used basis of testable hypotheses of how plants allocate resources. These concepts broadly state that plants increase biomass allocation to the plant parts that are involved in the acquisition of the most limiting resource. With the premise from above that plants normally are not C-limited in their natural environment (Körner 2003b; Millard et al. 2007), the concept of functional equilibrium predicts that the additional C fixed in a CO_2-enriched atmosphere is allocated to the root system for increased uptake of nutrients that are the supposedly most growth-limiting resources in this context. In line with this prediction, Norby et al. (2004) observed that an average increase in NPP of 22 % over the first 6 years of CO_2-enrichment was sustained by an increased production of fine root biomass in the Oak Ridge forest FACE. In the following 5 years of continued CO_2 enrichment, the initially expanding system of 10-year-old *Liquidambar styraciflua* trees at the beginning of the experiment (type II growth conditions according to Körner's 2006 classification) developed into a steady-state system (Körner's 2006 type III growth conditions) characterized by a fully explored soil and aerial space [fine root mass and leaf area index (LAI) remain stable]. In other words, the potential for fine roots exploring new resources reached its limit, and, consequently, the CO_2 effect on NPP decreased over time and was nil after 10 years of CO_2 enrichment (Norby et al. 2010). A shift to higher root biomass allocation is a common response to CO_2 enrichment in expanding type II systems (Hättenschwiler and Körner 1998; Iversen et al. 2008; Körner and Arnone 1992; Pritchard et al. 2008), but because this allocation pattern is temporary and changes with the degree of space (resource) exploration, the size of the CO_2 effect on NPP depends strongly on the time of harvest. In contrast, isometric biomass allocation (i.e. a constant relative amount of biomass is allocated to different plant parts) is expected in decoupled systems (Körner's 2006 type I growth conditions characterised by non-limiting resources) and in steady-state (type III) systems, regardless of the CO_2 effect on overall biomass production (typically large in type I and absent in type III). Accordingly, little or no CO_2 effect on biomass allocation is apparent in meta-analyses that notoriously treat all types of studies and growth conditions in the same way (Poorter et al. 2012; Wang and Taub 2010).

The question about where surplus C fixed under elevated CO_2 is allocated when CO_2 stimulation of leaf level photosynthesis persists with no apparent growth responses is more difficult to explain. There are basically two not mutually exclusive possibilities to explain this apparent mismatch between leaf-level C uptake and whole-plant biomass accumulation. The first is that leaf-level photosynthesis does not reflect well plant-level photosynthetic C uptake (see "The issue of the reference metric" below), and the second is that a higher C-input is often counteracted by increased C output (see "Fluxes are not pools" above). There is limited evidence that plants may respond to CO_2 enrichment with "morphological" or "phenological" downregulation at the plant canopy level, rather than with physiological downregulation of photosynthesis at the leaf level. Lower leaf area ratios (LAR, total leaf area per total plant biomass) (Callaway et al. 1994; Hättenschwiler and Körner 1998; Norby et al. 1992) and decreased branching and lower leaf area per unit branch biomass (Hättenschwiler et al. 1997a) indicate an increase in unproductive CO_2-respiring plant biomass relative to productive CO_2-assimilating leaf surface, and, thus, a reduction in the capacity of net CO_2 assimilation per unit plant biomass. In some instances, reduced LAR of individuals also translated to a reduction in leaf area index (LAI) at the community/stand level (Arnone and Körner 1995; Hättenschwiler and Körner 1998). These observations from artificially composed and enclosed model ecosystems have yet to be confirmed in long-term FACE studies (Körner et al. 2005; Liberloo et al. 2006; Norby et al. 2010) or at naturally CO_2-enriched sites (Hättenschwiler et al. 1997a) showing mostly no change in LAI. Phenological changes, such as delayed bud burst under elevated CO_2 (Hättenschwiler and Körner 1996; Murray et al. 1996) may further reduce the annual whole plant CO_2 uptake and greatly limit terrestrial NPP (Friend 2010). These results can never be captured by measuring leaf level photosynthesis during peak growing seasons. FACE studies, however, showed instead no CO_2 effects on phenology (Asshoff et al. 2006; Handa et al. 2005; Norby et al. 2003).

The second possibility of increased C outputs from plants grown in a CO_2-enriched atmosphere has received considerable attention and was particularly stimulating for research in soil ecology. The frequently observed higher rates of soil CO_2 efflux at elevated CO_2 (Spinnler et al. 2002; King et al. 2004; Körner et al. 2005; Jackson et al. 2009) indicate an increased belowground C allocation and faster C cycling through accelerated respiratory processes. Higher root biomass, increased fine root turnover, more C allocation to mycorrhizae, and higher heterotrophic microbial activity can all contribute individually or in combination to higher soil CO_2 efflux (Zak et al. 2000; King et al. 2004; Treseder 2004; Körner et al. 2005; Hagedorn et al. 2008; Jackson et al. 2009). The use of CO_2 from fossil fuel burning for experimental CO_2 enrichment results in a distinct $\delta^{13}C$ signature of mixed atmospheric CO_2 compared to current ambient air surrounding the vegetation, and thus has provided the possibility to follow newly acquired C through the plant and the ecosystem (e.g. von Felten et al. 2007; Keel et al. 2006). Analyses of ^{13}C showed that between 35 and 70 % of CO_2 in soil CO_2 efflux derives from recently assimilated, labile C sources (Keel et al. 2006; Taneva et al. 2006; Hagedorn et al. 2010), supporting the view of accelerated C cycling through the system rather than increased C storage in a CO_2-enriched atmosphere (Körner et al. 2005). Lower net ecosystem productivity (NEP: g C m^{-2} land area $year^{-1}$) values observed under elevated CO_2 at the desert FACE facility in Nevada also point to accelerated C cycling under high CO_2 (Jasoni et al. 2005). An increased availability of labile C in soils under elevated CO_2 was even observed to increase mineralisation of old soil C through priming

(Hagedorn et al. 2008; Langley et al. 2009) that may lead to soil C depletion in the longer term and perhaps greater C loss than uptake in a CO_2-enriched atmosphere.

Despite ample evidence for multiple pathways with contrasting fates of additional CO_2 fixed during leaf photosynthesis in a CO_2-enriched atmosphere, current papers continue introducing their study with overly simplified statements like "The primary effect of increasing CO_2 is photosynthetic enhancement in C_3 plants, and consequently increased plant productivity" (Erice et al. 2011). Such generalisation and simplification that neglects the complexity of interacting processes that determine C allocation within a plant, and across plant-associated organisms, and the ecosystem, continue the still widespread belief that leaf photosynthesis equals plant biomass production and ecosystem NPP. It also leads to the unreasonable belief that overcoming CO_2 limitation of photosynthesis by molecular engineering might hold some answers to the pressing question of how to cope with global change and growing human populations (Leakey and Lau 2012). The agricultural literature has acknowledged for some time that plant C-allocation and not leaf photosynthesis is the key process determining plant growth, biomass production and yield (Gifford and Evans 1981; Wardlaw 1990).

The issue of the reference metric

The indication of some quantity (e.g. the average daily water consumption of 575 l per person living in the US) per se does not mean a lot but requires a reference for a meaningful interpretation. For example, we may compare this quantity of water with the same data from other countries such as Germany (200 l per person and per day) or Nigeria (40 l per person and per day), or refer to the total available potable water or the percent use of annual reserves. The choice and use of an appropriate reference metric is critical for putting this quantity of water into context. In ecology, the reference or denominator is often a unit surface area, a time period, an individual or a combination of those. The difference in referring a measurement to one or another reference metric often represents the impact of a third (sometimes unknown) variable. For example, GDP (the Gross Domestic Product) can be expressed per capita, or per citizen, the difference between the two indicating the number of foreign workers in a country. In ecology, the arctic tundra becomes as productive as the tropics if productivity is expressed per month during the growing season instead of per year (Körner 1999). In this example, using a yearly reference period tells us about the growing season length (a third variable), rather than the system's potential to produce biomass.

Classic and meanwhile relatively well-understood examples from CO_2 research are estimates of C fluxes in ecosystems under ambient and elevated CO_2. The question of what temporal and spatial scales those C fluxes are referred to is key, as it determines how results from small-scale CO_2 experiments relate to larger temporal and spatial scales and the possibility to predict future long-term responses. Photosynthesis data from elevated CO_2 experiments are usually expressed per unit leaf area per second of sunlit leaves, i.e. relative to a high-resolution spatiotemporal reference. Such data cannot easily be scaled to photosynthesis per unit ground area and year unless the leaf area index and photosynthetic rates in the sub-canopy layers are known. Extrapolating to larger time scales, it makes a big difference whether we express photosynthetic rates per second, per day or per year. In the case of elevated CO_2 experiments, the measurements are usually taken at optimal conditions (peak season, fully sunlit leaves) and the obtained CO_2 response unlikely represents the average per day, per month or per season. For technical reasons, the choices of reference metrics are often restricted (measuring C fluxes on a leaf is easier than measuring ecosystem C fluxes). The challenge is therefore to anticipate and assess the relevance of the measurements in a larger context of various (potential) reference metrics across different temporal and spatial scales. The importance of the spatial scale is nicely illustrated by a study on tree water relationships under elevated CO_2. Tricker et al. (2009) observed a decrease in leaf-level transpiration, but an increase in stand-level transpiration in response to elevated CO_2. The differences in the measurements at different spatial scales were due to an increased LAI relative to the control. Consequently, depending on the reference metric (leaf-level vs. stand-level), the obtained net water fluxes in response to elevated CO_2 showed opposite signs.

Generally, for larger spatiotemporal reference metrics, e.g. longer reference periods, the measurement of an increasing number of processes and variables must be considered in order to account for a wider spectrum of environmental conditions and variability. Usually, short-term effect sizes tend to be reduced if referred to larger reference metrics (Körner 2006). For example, the often positive CO_2 effect on plant C uptake measured at small spatial and temporal scales decreases as larger reference areas and periods are considered (Field et al. 1995; Körner et al. 2007; Table 1). The reasons for these differences are not always obvious, but may include allometric shifts at the individual plant level that are not captured by leaf-level measurements (e.g. Hättenschwiler and Körner 1996) or may integrate across different processes (atmospheric feedback, seasonality, extreme events) whose relative impacts are more important at larger scales (Leuzinger et al. 2011).

Table 1 The reference metric matters: plant response to increased spatial scale, overview of meta-analyses and reviews on plant carbon uptake at the leaf level and at the plant level under elevated CO_2. On average, responses are larger at the smaller scale

Reference	Plants studied	Method of CO_2-enrichment	Increase in CO_2 applied	Leaf level response			Plant level response		
				Parameter	Number of studies	% mean increase under CO_2	Parameter	Number of studies	% mean increase under CO_2
Ainsworth and Rogers (2007)	C_3 plants	FACE	Mean = 567 ppm	A	439	31			
Ceulemans and Mousseau (1994)	Woody plants	P, GH, OTC		A per leaf area	55	50.5	Total biomass	98	50.5
Curtis and Wang (1998)	Woody plants	GC, GH, OTC	600–800 ppm	A	69	40.5	Total biomass	102	28.8 ± 2.4 SE
Norby et al. (1999)	Trees	OTC, FACE	Ambient + 300 ppm	A	37	66	Wood increm. per leaf area	13	27
de Graaff et al. (2006)	All plants	OTC, FACE	430-750 ppm				Total biomass	117	25
5 forest FACE studies[a]	Trees	FACE	Mean = 550 ppm	A		42.7 ± 3.8 SE			23 ± 1.3 SE
Average value						46	Average value		31

A net photosynthesis rate, *P* potted plants, *GH* green house, *GC* growth chamber, *OTC* open top chamber

[a] Forest face sites that ran for a minimum of 8 years and with appropriate data published were selected (ORNL FACE, DukeFACE and data from the Swiss Canopy Crane, SCC). Data were extracted from Norby et al. (2005) with updates from the north American forest-FACE synthesis website http://public.ornl.gov/face/npp_synthesis.shtml. SCC data are from Körner et al. (2005), updated by unpublished data (M. Bader, personal communication)

A slightly different nuance of the ‘reference metric issue’ occurs when a response to CO_2 or another treatment is observed at a given scale, but disappears at a larger scale. This might be due to experimental artefacts inherent to the relatively small scale of many experiments. We raise the following question as an illustration of this problem: is tropical rainforest productivity limited by light availability? We would probably say yes, and the literature would back this up (e.g. Boisvenue and Running 2006). If we were providing a series of plots of tropical rainforest with additional light, we would indeed observe an increased plant C uptake and maybe increased plant growth, and perhaps even a higher amount of carbon stored per unit ground area within the light-treated plots compared to unchanged control plots. However, we argue that this response would not be observed at the landscape scale because important feedback effects may not play out at the scale of relatively small plots for such an experiment. For example, at constant intrinsic plant water use efficiency, we would necessarily measure higher stand transpiration with increased productivity. This would entail higher air humidity and important atmospheric feedback at the landscape scale that would not be expressed at the scale of experimental plots. Another problem with relatively small experimental plots are ‘edge effects’ (Ries and Sisk 2004). In our example, experimental plots would be surrounded by non-light-enriched vegetation. Consequently, plants in experimental plots could extend their canopies along the edges of non-treated vegetation leading to increased growth at the plot level, which would not be possible if additional light was available at the landscape scale.

In summary, we showed that the metric any measurements are referred to (e.g. ‘per leaf’, ‘per unit surface area’, ‘per day’, or ‘per season’) deserve critical consideration both while planning and interpreting experiments in ecology. The two main reasons for this are: (1) ecological processes can be misinterpreted if they are expressed on the basis of an inappropriate reference metric; and (2) we may observe artefacts if we consider the wrong reference metrics such as the plot instead of the landscape scale.

The role of time and timing

'Time' and 'timing' are fundamental components of ecological thinking, and yet they are often overlooked as key explanatory variables for observed phenomena. Examples are the age of (experimental) individuals, communities, soils, the duration of an experiment, the timing (time of day, season, temporal replication) of measurements, and the time period over which measurements are integrated, scaled up, and interpreted. Often, we fail to explicitly refer our findings to an appropriate temporal context. All ecological processes are dynamic and in constant transition, and thus all observations and measurements require some measure of time or reference to temporal scale (cf. section above).

The change in atmospheric CO_2 concentration itself is transient with a continuous increase and a long-term shift in the mean concentration. Somewhat different compared to rising atmospheric CO_2, changes in temperature and precipitation will show changes both in the mean and variance. Heat waves and extreme precipitation events can thus be simulated in a manner that is closer to realistic predictions than CO_2 experiments in which a step increase in CO_2 concentration must be imposed. This is an unavoidable caveat of any experiment with elevated atmospheric CO_2. Modelling the difference between a step and a gradual change in CO_2 suggests a rather unrealistic initial peak in photosynthesis and carbon sequestration, the latter declining sharply in the first few years of elevated CO_2 (Luo and Reynolds 1999). Experiments confirm that initial peaks in CO_2 responses (e.g. in plant growth, water use efficiency) tend to be larger than long-term responses (Kimball et al. 2007; Körner et al. 2005; Norby 2010; Leuzinger et al. 2011). The reasons for this are largely of a stoichiometric nature because nutrients become increasingly limiting (see "The stoichiometry issue" above), and of an ecophysiological nature because plants acclimate to altered conditions over time.

Long-term exposure to elevated CO_2 could trigger shifts in species composition if even closely related species show different responses (Handa et al. 2006). For example, if a particular species benefits more from elevated CO_2, it may eventually replace other species that took less advantage of elevated CO_2 (Langley and Megonigal 2010). The net CO_2 response in terms of ecosystem C and H_2O fluxes then not only depends on the physiological response of the current species assemblage but also on the vegetation dynamics triggered by elevated CO_2 (or even other global change drivers that occur concurrently). Such long-term effects are difficult to test, particularly with long-lived species, but the potential heuristic value of these experiments should not be overlooked.

Another time-dependent issue that may cause erroneous conclusions is successional dynamics and the time of arrival of particular plant species. Apparent impacts of environmental variables (e.g. CO_2, temperature) can potentially be determined by the timing of the arrival and loss of different species (either due to natural succession or to management), or of the site history (management, soil properties, atmospheric nitrogen and dust deposition). Körner et al. (2008), for example, show that, with herbaceous species, the time of sowing (or of seed arrival in a natural setting) can have long-lasting dominance effects, even after substantial above-ground disturbance. Such timing and historic effects are even more difficult to detect and disentangle in forest ecosystems, as the time scales and response times far exceed the average human lifespan (Bernal et al. 2012). The longer lifespan of trees as opposed to that of herbaceous plants also complicates analyses because responses may differ according to the ontogenetic stage of an organism, and a tree's full ontogeny cannot realistically be covered in any experiment. In the case of elevated atmospheric CO_2, responses tend to decrease with tree age (Hättenschwiler et al. 1997b; Voelker et al. 2006). However, a recent observational field study with ponderosa pine suggested that increasing atmospheric CO_2 might be driving increased growth of old-growth forests (Knapp and Soule 2011). Because the majority of CO_2 experiments were/are conducted with young trees or seedlings, they may overestimate forest tree responses to rising CO_2. Ontogeny-related changes in CO_2 responses are also affected by scaling issues and stoichiometry (Leuzinger et al. 2011), and their relative importance is not easily separated.

In summary, statements on C pools and fluxes need to be evaluated on a specific time scale, similar to the mean residence time of C in a pool (Körner 2006; Luo and Weng 2011). This principle is equally valid for other measures of fluxes and pools of materials, elements and energy in an ecological context. Second, the ontogenetic stage of the experimental organism is almost always key to the experimental outcome, irrespective of the parameters under consideration.

Second-order and confounding effects

In ecology, the unequivocal determination of cause and effect in observed patterns is one of the key challenges. Correlations are readily observed (e.g. the relationships 'number of species–latitude', or 'treeline–altitude'), but causal explanations based on driving mechanisms are often heavily debated (Sherratt and Wilkinson 2010). Two omnipresent pitfalls are (1) the observed correlation is coincidental, the classic and illustrative example being the correlation between storks and birth rates (Matthews 2000) and (2) the correlation is causal, but second-order effects may mitigate or reverse a first-order response. For example, Scheffer et al. (2006) reported that the lower biodiversity in fish species in small versus large ponds leads to a larger overall biodiversity (beyond fish) in small ponds because of the absence of predation on invertebrates by certain fish species. This stands in contrast to (but is a consequence of) the paradigm that smaller, more disrupted habitats (here the smaller ponds) harbour fewer species.

We find examples for both of these pitfalls in CO_2 research. Confounding effects may occur because atmospheric CO_2 changes in concert with other environmental changes. For example, the change in stable isotope levels, as an indicator of intrinsic water use efficiency (iWUE), and increases in tree growth rates during the twentieth century have sometimes been attributed to elevated atmospheric CO_2 (Feng 1999; Knapp and Soule 2011). However, concurrent changes of other environmental parameters over the past century (mean temperature, nitrogen deposition, land-use, species composition) may have all influenced stable isotope signatures and tree growth. This makes it almost impossible to tease apart the relative effects of simultaneously changing environmental conditions to prove that the observed change in tree growth is caused by rising atmospheric CO_2. Additionally, iWUE is a ratio, which can change as a result of changes in either the numerator or denominator, so that a simultaneous increase in iWUE and growth may not be related (e.g. if there is a concurrent change in plant water loss).

A long-lasting confusion exists for the relationship between plant growth and photosynthesis. It is often assumed that photosynthesis drives plant growth (see also "Fluxes are not pools" above). Plant growth and photosynthesis per unit leaf area may well correlate, but this does not mean that there is a causal and directional relationship (from photosynthesis to growth). For example, in cold, and dry environments, photosynthesis per unit leaf area may be comparable to that measured in other more favourable environments, but growth of individual plants is slow. In cold (Hoch and Körner 2003; Hoch and Körner 2012; Hoch et al. 2002; Oberhuber et al. 2011) and dry (Körner 2003b; Muller et al. 2011) environments, mobile C reserves tend to accumulate and are not used for growth, because under these conditions plant tissue expansion and therefore 'growth' is controlled by temperature and water availability, but not by the rate of leaf-level C uptake. Nevertheless, most global dynamic vegetation models (Cramer et al. 2001) still use photosynthesis as the driving force of plant growth, even under temperature- and water-limited conditions.

Second-order effects occur when an immediate response to elevated atmospheric CO_2 triggers a secondary, eventually dominating response. For example, plant transpiration is unavoidably affected if stomatal opening changes in response to elevated CO_2. Such stomatal responses have far-reaching consequences for soil water content, air humidity and hence soil and atmospheric feedback (Jacobs and de Bruin 1997). Holtum and Winter (2010) argue that the secondary water effect may in many cases become more important than the first-order CO_2 effect. Lower water use per plant individual in response to elevated CO_2 can persist with an accumulating effect over time (Niklaus et al. 1998). The indirect or second-order CO_2 effect via increased plant water savings followed by higher soil humidity can then be the dominant CO_2 effect on community biomass production with particularly strong relative CO_2 effects in dry years and weaker relative CO_2 effects in moist years (Niklaus and Körner 2004; Morgan et al. 2004). Moreover, different species may show different responses to elevated CO_2 in terms of water savings. In a calcareous grassland in Switzerland, for example, the dominant species *Bromus erectus* drastically reduced stomatal conductance under elevated CO_2, while the subordinate species *Carex flacca* did not (Lauber and Körner 1997). The overall decreased community transpiration and increased soil water content (Niklaus et al. 1998; Niklaus and Körner 2004) was, nevertheless, particularly beneficial for *Carex flacca* with an increase in above-ground biomass of more than 300 % compared to ambient CO_2 control plots (Niklaus and Körner 2004). The water saver *Bromus erectus*, on the other hand, showed no biomass response to elevated CO_2 which in the long term may suggest decreasing *Bromus* abundance at the expense of the "water waster" *Carex* (Niklaus and Körner 2004). This example nicely illustrates the intricate relationships between primary causes, second-order effects and complex consequences that may lead to changes in community composition and ecosystem functioning that are difficult to predict.

The distinction of causes and effects and their mechanistic understanding is fundamental in ecology in order to predict current and future ecosystem structure and functioning with the help of modelling tools. Model algorithms based on correlative evidence rather than on causal relationships may be particularly prone to misleading interpretations and predictions of future responses.

The biodiversity issue

Biodiversity relates to all six topics that have been treated so far, and may be the most important aspect to consider when studying ecological processes at the level of communities and ecosystems. This is because organisms inherently possess a wide variety of physiological, anatomical, and evolutionary traits that a shift in species assemblage over time may render any conclusions based on a static community structure invalid. For example, biodiversity shifts may affect the balance between carbon fluxes and pools (e.g. if forest is transformed into steppe). Similarly, shifts in biodiversity may overcome stoichiometric constraints if the replacing plant community is characterised by different elemental ratios. Plant responses to global change, or any other ecological process, should be assessed using a range of different species, explicitly asking how and why species differ and whether a shift in the present species composition is likely and what it would mean for the net ecosystem response. For example, responses to drought during the European 2003 heat wave were dramatic in hornbeam (*Carpinus betulus*), but absent in oak (*Quercus petraea*), such that overall (long-term) landscape-level responses depended on both the physiological response of individuals and on the longer-term species composition (Leuzinger et al. 2005). Biodiversity shifts dominating physiological responses of individuals to elevated CO_2 have been documented for herbaceous plants in a brackish wetland. Within only a few years, N addition caused the less CO_2-responsive C_4 species to dominate over the more CO_2-responsive C_3 species, thus eradicating the first-order CO_2 effect through a change in species composition (Langley and Megonigal 2010). Similar processes are to be expected in trees over longer time spans. In fact, germinating seedlings of co-occurring temperate forest tree species showed highly contrasting growth responses to in situ CO_2 enrichment applied using open-top chambers in the forest understory, that also depended on light availability (Hättenschwiler and Körner 2000; Hättenschwiler and Körner 2003). Initial tree seedling growth just after germination critically determines the regeneration success and future canopy composition of forests (Clark and Clark 1992; Kobe et al. 1995). Consequently, the strong differences among species in seedling growth response to elevated CO_2 will affect community composition in the longer term (Bolker et al. 1995). Particularly strong growth responses to elevated CO_2 in shaded forest understory conditions were observed for lianas (Granados and Körner 2002; Hättenschwiler and Körner 2003), suggesting accelerated forest dynamics in tropical forests, that are particularly rich in lianas, through increased rates of forest gap formation (Körner 2009b). As a consequence, the relative abundance of early successional tree species will likely increase, and overall these biodiversity effects may reduce C sequestration, thus overriding potential direct effects predicted with a static species composition of tropical forest communities.

Table 2 Checklist of questions according to the seven topics discussed

Topic	Question
I Fluxes are not pools	Are we measuring fluxes or pools?
	How important is the observed flux relative to the pool of interest?
	Are there compensatory fluxes to the one measured that may be less apparent or difficult to measure?
	Is the change in flux measured persistent over time? (see V)
II Stoichiometry	Are factors other than the one(s) considered becoming limiting?
	Does the experiment allow enough time for stoichiometric ratios to equilibrate or do we observe an initial transient response? (see V)
III Resource allocation	What is the potential for allocation shifts in the studied system? How could/should allocation be measured/quantified (methodology)?
	Does altered resource allocation modify the relative importance of pools and fluxes? (see I)
	Are trophic interactions influenced by allocation shifts and could this lead to overriding second-order effects? (see VI)
IV Reference metric	Are we choosing the appropriate reference metric in terms of time and space? (see V)
	Would the observations be the same if a larger context were chosen? Would other processes become important that are not observable at the smaller scale? (see VI and VII)
V Time and timing	What time span/time horizon are the observations likely to be valid for? (What is the appropriate reference metric? (see III)
	Would the same effect be observed if a different ontogenetic stage of the studied organism was considered?
	Can historic confounding effects (e.g. time of seed arrival) be excluded?
VI Second order effects	Are the observed responses direct consequences of the treatment or does the treatment correlate with some other factor that is driving the response?
	Are the observed effects primary or perhaps second-order effects? Are different or additional measurements required for the distinction of primary versus second-order effects?
	Is there a cascade of effects triggered by the treatment, and at what stage are we observing our response? Will it persist over time? (see V)
VII Biodiversity	Would the measured response be the same if other species were tested?
	Do the species included in the test allow a general comparative assessment of responses? (e.g. are plant functional types tested?)
	How likely (and in what time frame) is a treatment-induced species composition shift? (see V)

Conclusions

The past 25 years of CO_2 research have taught us beyond future ecosystem functioning, and a lot of the lessons learnt bear a general ecological relevance. Here, we focus on the contribution of the research group under Christian Körner, grouping some general insights into seven cornerstones for a sound basis to plan and interpret experiments and modelling studies, not only in CO_2 research but also beyond. We have summarised the key questions that can help with the planning and interpretation of ecological experiments and model frameworks in Table 2. While it is impossible to weight all points equally, this paper attempts to raise awareness of potential confusion, restrictions and pitfalls, the recognition of which can make ecological research more efficient. Overall, we conclude that ignorance of the issues raised here is more likely to cause overestimation than underestimation of effect sizes on various ecological processes in response to global environmental change.

Acknowledgments We thank an anonymous reviewer for helpful comments on the text. S.L. received funding from the FP7 project 'ACQWA'.

References

Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO(2) enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy. New Phytol 165:351–371

Ainsworth EA, Rogers A (2007) The response of photosynthesis and stomatal conductance to rising [CO2]: mechanisms and environmental interactions. Plant Cell Environ 30:258–270

Arnone JA, Körner C (1995) Soil and biomass carbon pools in model communities of tropical plants under elevated CO_2. Oecologia 104:61–71

Asshoff R, Zotz G, Körner C (2006) Growth and phenology of mature temperate forest trees in elevated CO_2. Glob Change Biol 12:848–861

Bazzaz FA, Grace J (1997) Plant resource allocation. Academic, San Diego

Bernal S, Hedin LO, Likens GE, Gerber S, Buso DC (2012) Complex response of the forest nitrogen cycle to climate change. Proc Natl Acad Sci USA 109:3406–3411

Bloom AJ, Chapin FS III, Mooney HA (1985) Resource limitation in plants—an economic analogy. Annu Rev Ecol Syst 16:363–392

Boisvenue C, Running SW (2006) Impacts of climate change on natural forest productivity—evidence since the middle of the 20th century. Glob Change Biol 12:862–882

Bolker BM, Pacala SW, Bazzaz FA, Canham CD, Levin SA (1995) Species-diversity and ecosystem response to carbon-dioxide fertilization—conclusions from a temperate forest model. Glob Change Biol 1:373–381

Brouwer R (1962) Distribution of dry matter in the plant. Netherlands. J Agric Sci 10:361–376

Callaway RM, DeLucia EH, Thomas EM, Schlesinger WH (1994) Compensatory responses of CO_2 exchange and biomass allocation and their effects on the relative growth-rate of ponderosa pine in different CO_2 and temperature regimes. Oecologia 98:159–166

Ceulemans R, Mousseau M (1994) Tansley Review No-71—effects of elevated atmospheric CO_2 on woody-plants. New Phytol 127:425–446

Chapin FS III, McFarland J, McGuire AD, Euskirchen ES, Ruess RW, Kielland K (2009) The changing global carbon cycle: linking plant-soil carbon dynamics to global consequences. J Ecol 97:840–850

Clark DA, Clark DB (1992) Life-history diversity of canopy and emergent trees in a neotropical rain-forest. Ecol Monogr 62:315–344

Cohen L (1988) Everybody Knows. I'm Your Man. Sony Music Entertainment (Canada) Inc., Toronto

Cramer W et al (2001) Global response of terrestrial ecosystem structure and function to CO_2 and climate change: results from six dynamic global vegetation models. Glob Change Biol 7:357–373

Curtis PS, Wang XZ (1998) A meta-analysis of elevated CO_2 effects on woody plant mass, form, and physiology. Oecologia 113:299–313

de Graaff M-A, van Groenigen K-J, Six J, Hungate B, van Kessel C (2006) Interactions between plant growth and soil nutrient cycling under elevated CO_2: a meta-analysis. Glob Change Biol 12:2077–2091

Drake JE et al (2011) Increases in the flux of carbon belowground stimulate nitrogen uptake and sustain the long-term enhancement of forest productivity under elevated CO(2). Ecol Lett 14:349–357

Elser JJ et al (2000) Biological stoichiometry from genes to ecosystems. Ecol Lett 3:540–550

Erice G, Sanz-Sáez A, Aranjuelo I, Irigoyen JJ, Aguirreolea J, Avice J-C, Sánchez-Díaz M (2011) Photosynthesis, N_2 fixation and taproot reserves during the cutting regrowth cycle of alfalfa under elevated CO_2 and temperature. J Plant Physiol 168:2007–2014

Feng XH (1999) Trends in intrinsic water-use efficiency of natural trees for the past 100–200 years: a response to atmospheric CO2 concentration. Geochim Cosmochim Acta 63:1891–1903

Field CB, Jackson RB, Mooney HA (1995) Stomatal responses to increased CO_2: implications from the plant to the global scale. Plant Cell Environ 18:1214–1225

Finzi AC, Moore DJP, DeLucia EH, Lichter J, Hofmockel KS, Jackson RB, Hyun-Seok K, Matamala R, McCarthy HR, Oren R, Pippen JS, Schlesinger WH (2006) Progressive nitrogen limitation of ecosystem processes under elevated CO_2 in a warm-temperate forest. Ecology 87:15–25

Friend AD (2010) Terrestrial plant production and climate change. J Exp Bot 61:1293–1309

Gedroc JJ, McConnaughay KDM, Coleman JS (1996) Plasticity in root shoot partitioning: optimal, ontogenetic, or both? Funct Ecol 10:44–50

Gifford RM, Evans LT (1981) Photosynthesis, carbon partitioning, and yield. Annu Rev Plant Physiol Plant Mol Biol 32:485–509

Granados J, Körner C (2002) In deep shade, elevated CO_2 increases the vigor of tropical climbing plants. Glob Change Biol 8:1109–1117

Hagedorn F, van Hees PAW, Handa IT, Hättenschwiler S (2008) Elevated CO_2 fuels leaching of old dissolved organic matter at the alpine treeline. Glob Biogeochem Cycles 22:GB2004. doi: 10.1029/2007GB003026

Hagedorn F, Martin M, Rixen C, Rusch S, Bebi P, Zürcher A, Siegwolf RTW, Wipf S, Escape C, Roy J, Hättenschwiler S (2010) Short-term responses of ecosystem carbon fluxes to experimental soil warming at the Swiss alpine treeline. Biogeochemistry 97:7–19

Handa IT, Körner C, Hattenschwiler S (2005) A test of the tree-line carbon limitation hypothesis by in situ CO_2 enrichment and defoliation. Ecology 86:1288–1300

Handa IT, Körner C, Hättenschwiler S (2006) Conifer stem growth at the altitudinal treeline in response to four years of CO_2 enrichment. Glob Change Biol 12:2417–2430

Hättenschwiler S, Körner C (1996) System-level adjustments to elevated CO_2 in model spruce ecosystems. Glob Change Biol 2:377–387

Hättenschwiler S, Körner C (1998) Biomass allocation and canopy development in spruce model ecosystems under elevated CO_2 and increased N deposition. Oecologia 113:104–114

Hättenschwiler S, Körner C (2000) Tree seedling responses to in situ CO_2-enrichment differ among species and depend on understorey light availability. Glob Change Biol 6:213–226

Hättenschwiler S, Körner C (2003) Does elevated CO_2 facilitate naturalization of the non-indigenous *Prunus laurocerasus* in Swiss temperate forests? Funct Ecol 17:778–785

Hättenschwiler S, Miglietta F, Raschi A, Körner C (1997a) Morphological adjustments of mature *Quercus ilex* trees to elevated CO_2. Acta Oecol 18:361–365

Hättenschwiler S, Miglietta F, Raschi A, Körner C (1997b) Thirty years of in situ tree growth under elevated CO_2: a model for future forest responses? Glob Change Biol 3:463–471

Hoch G, Körner C (2003) The carbon charging of pines at the climatic treeline: a global comparison. Oecologia 135:10–21

Hoch G, Körner C (2012) Global patterns of mobile carbon stores in trees at the high-elevation tree line. Glob Ecol Biogeogr 21:861–871

Hoch G, Popp M, Körner C (2002) Altitudinal increase of mobile carbon pools in *Pinus cembra* suggests sink limitation of growth at the Swiss treeline. Oikos 98:361–374

Holtum JAM, Winter K (2010) Elevated CO_2 and forest vegetation: more a water issue than a carbon issue? Funct Plant Biol 37:694–702

Idso SB, Kimball BA (1993) Tree growth in carbon-dioxide enriched air and its implications for global carbon cycling and maximum levels of atmospheric CO_2. Glob Biogeochem Cycles 7:537–555

IPCC (2007) Climate change 2007: fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge

Iversen CM, Ledford J, Norby RJ (2008) CO(2) enrichment increases carbon and nitrogen input from fine roots in a deciduous forest. New Phytol 179:837–847

Iversen CM, Hooker TD, Classen AT, Norby RJ (2011) Net mineralization of N at deeper soil depths as a potential mechanism for sustained forest production under elevated CO(2). Glob Change Biol 17:1130–1139

Jackson RB, Cook CW, Pippen JS, Palmer SM (2009) Increased belowground biomass and soil CO_2 fluxes after a decade of carbon dioxide enrichment in a warm-temperate forest. Ecology 90:3352–3366

Jacobs CMJ, de Bruin HAR (1997) Predicting regional transpiration at elevated atmospheric CO_2: influence of the PBL-vegetation interaction. J Appl Meteorol 36:1663–1675

Jasoni RL, Smith SD, Arnone JA (2005) Net ecosystem CO2 exchange in Mojave Desert shrublands during the eighth year of exposure to elevated CO_2. Glob Change Biol 11:749–756

Keel S, Siegwolf RTW, Körner C (2006) Canopy CO_2 enrichment permits tracing the fate of recently assimilated carbon in a mature deciduous forest. New Phytol 172:319–329

Kimball BA, Mauney JR, Nakayama FS, Idso SB (1993) Effects of increasing atmospheric CO_2 on vegetation. Vegetation 104:65–75

Kimball BA, Idso SB, Johnson S, Rillig MC (2007) Seventeen years of carbon dioxide enrichment of sour orange trees: final results. Glob Change Biol 13:2171–2183

King JS, Hanson PJ, Bernhardt E, DeAngelis P, Norby RJ, Pregitzer KS (2004) A multiyear synthesis of soil respiration responses to elevated atmospheric CO_2 from four forest FACE experiments. Glob Change Biol 10:1027–1042

Knapp PA, Soule PT (2011) Increasing water-use efficiency and age-specific growth responses of old-growth ponderosa pine trees in the Northern Rockies. Glob Change Biol 17:631–641

Kobe RK, Pacala SW, Silander JA, Canham CD (1995) Juvenile tree survivorship as a component of shade tolerance. Ecol Appl 5:517–532

Körner C (1999) Alpine plants: stressed or adapted? In: Press MC, Scholes JD, Barker MG (eds) Physiological plant ecology. Blackwell, Oxford, pp 297–311

Körner C (2003a) Alpine plant life: functional plant ecology of high mountain ecosystems. Springer, Berlin

Körner C (2003b) Carbon limitation in trees. J Ecol 91:4–17

Körner C (2003c) Ecological impacts of atmospheric CO_2 enrichment on terrestrial ecosystems. Philos Trans R Soc Lond A 361:2023–2041

Körner C (2003d) Slow in, rapid out—carbon flux studies and Kyoto targets. Science 300:1242–1243

Körner C (2006) Plant CO_2 responses: an issue of definition, time and resource supply. New Phytol 172:393–411

Körner C (2009a) Biological Carbon sinks: turnover must not be confused with capital! Gaia-Ecol Perspect Sci Soc 18:288–293

Körner C (2009b) Responses of humid tropical trees to rising CO(2). Annu Rev Ecol Evol Syst 40:61–79

Körner C, Arnone JA (1992) Responses to elevated carbon dioxide in artificial tropical ecosystems. Science 257:1672–1675

Körner C et al (2005) Carbon flux and growth in mature deciduous forest trees exposed to elevated CO_2. Science 309:1360–1362

Körner C, Morgan J, Norby R (2007) Terrestrial ecosystems in a changing world. CO_2 fertilization: when, where, how much?. Springer, Berlin

Körner C, Stöcklin J, Reuther-Thiebaud L, Pelaez-Riedl S (2008) Small differences in arrival time influence composition and productivity of plant communities. New Phytol 177:698–705

Langley JA, Megonigal JP (2010) Ecosystem response to elevated CO_2 levels limited by nitrogen-induced plant species shift. Nature 466:96–99

Langley JA, McKinley DC, Wolf AA, Hungate BA, Drake BG, Megonigal JP (2009) Priming depletes soil carbon and releases nitrogen in a scrub-oak ecosystem exposed to elevated CO_2. Soil Biol Biochem 41:54–60

Lauber W, Körner C (1997) In situ stomatal responses to long-term CO_2 enrichment in calcareous grassland plants. Acta Oecol 18:221–229

Le Quere C et al (2009) Trends in the sources and sinks of carbon dioxide. Nat Geosci 2:831–836

Leakey ADB, Lau JA (2012) Evolutionary context for understanding and manipulating plant responses to past, present, and future atmospheric [CO2]. Philos Trans R Soc Lond B 367:613–629

Leuzinger S, Zotz G, Asshoff R, Korner C (2005) Responses of deciduous forest trees to severe drought in Central Europe. Tree Physiol 25:641–650

Leuzinger S, Luo YQ, Beier C, Dieleman W, Vicca S, Korner C (2011) Do global change experiments overestimate impacts on terrestrial ecosystems? Trends Ecol Evol 26:236–241

Liberloo M et al (2006) Woody biomass production during the second rotation of a bio-energy Populus plantation increases in a future high CO_2 world. Glob Change Biol 12:1094–1106

Luo YQ, Reynolds JF (1999) Validity of extrapolating field CO_2 experiments to predict carbon sequestration in natural ecosystems. Ecology 80:1568–1583

Luo Y, Weng E (2011) Dynamic disequilibrium of the terrestrial carbon cycle under global change. Trends Ecol Evol 26:96–104

Luo Y et al (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. Bioscience 54:731–739

Luo YQ et al (2011) Coordinated approaches to quantify long-term ecosystem dynamics in response to global change. Glob Change Biol 17:843–854

Matthews R (2000) Storks Deliver Babies ($p = 0.008$). Teach Stat 22:36–38

Millard P, Sommerkorn M, Grelet G-A (2007) Environmental change and carbon limitation in trees: a biochemical, ecophysiological and ecosystem appraisal. New Phytol 175:11–28

Morford SL, Houlton BZ, Dahlgren RA (2011) Increased forest ecosystem carbon and nitrogen storage from nitrogen rich bedrock. Nature 477:U78–U88

Morgan JA, Pataki DE, Körner C, Clark H, Del Grosso SJ, Grünzweig JM, Knapp AK, Mosier AR, Newton PCD, Niklaus PA, Nippert JP, Nowak RS, Parton WJ, Polley HW, Shaw MR (2004) Water relations in grassland and desert ecosystems exposed to elevated CO_2. Oecologia 140:11–25

Muller B et al (2011) Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and growth in sink organs. J Exp Bot 62:1715–1729

Murray MB, Leith ID, Jarvis PG (1996) The effect of long term CO2 enrichment on the growth, biomass partitioning and mineral nutrition of Sitka spruce (*Picea sitchensis* (Bong) Carr). Trees Struct Funct 10:393–402

Niklaus PA, Körner C (2004) Synthesis of a six-year study of calcareous grassland responses to in situ CO_2 enrichment. Ecol Monogr 74:491–511

Niklaus PA, Spinnler D, Körner C (1998) Soil moisture dynamics of calcareous grassland under elevated CO_2. Oecologia 117:201–208

Norby RJ (2010) ORNL net primary productivity data, Oak Ridge National Laboratory. In: Carbon Dioxide Information Analysis Center, U.S. Department of Energy. http://cdiac.ornl.gov

Norby RJ, Zak DR (2011) Ecological lessons from free-air CO_2 enrichment (FACE) experiments. Annu Rev Ecol Evol Syst 42(42):181–203

Norby RJ, Gunderson CA, Wullschleger SD, Oneill EG, McCracken MK (1992) Productivity and compensatory responses of yellow-poplar trees in elevated CO_2. Nature 357:322–324

Norby RJ, Wullschleger SD, Gunderson CA, Johnson DW, Ceulemans R (1999) Tree responses to rising CO_2 in field experiments: implications for the future forest. Plant Cell Environ 22:683–714

Norby RJ, Hartz-Rubin JS, Verbrugge MJ (2003) Phenological responses in maple to experimental atmospheric warming and CO_2 enrichment. Glob Change Biol 9:1792–1801

Norby RJ, Ledford J, Reilly CD, Miller NE, O'Neill EG (2004) Fine-root production dominates response of a deciduous forest to atmospheric CO_2 enrichment. Proc Natl Acad Sci USA 101:9689–9693

Norby RJ et al (2005) Forest response to elevated CO_2 is conserved across a broad range of productivity. Proc Natl Acad Sci USA 102:18052–18056

Norby RJ, Warren JM, Iversen CM, Medlyn BE, McMurtrie RE (2010) CO(2) enhancement of forest productivity constrained by limited nitrogen availability. Proc Natl Acad Sci USA 107:19368–19373

Oberhuber W, Swidrak I, Pirkebner D, Gruber A (2011) Temporal dynamics of nonstructural carbohydrates and xylem growth in *Pinus sylvestris* exposed to drought. Can J For Res Rev Canadienne De Recherche Forestiere 41:1590–1597

Oren R et al (2001) Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-enriched atmosphere. Nature 411:469–472

Petit JR, Jouzel J, Raynaud D, Barkov NI, Barnola JM, Basile I, Bender M, Chappellaz J, Davis M, Delaygue G, Delmotte M, Kotlaykov VM, Legrand M, Lipenkov VY, Lorius C, Pepin L, Ritz C, Saltzman E, Stievenard M (1999) Nature 399:429–436

Polis GA (1999) Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. Oikos 86:3–15

Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytol 193:30–50

Pritchard SG, Strand AE, McCormack ML, Davis MA, Oren R (2008) Mycorrhizal and rhizomorph dynamics in a loblolly pine forest during 5 years of free-air-CO_2-enrichment. Glob Change Biol 14:1252–1264

Redfield AC (1958) The biological control of chemical factors in the environment. Am Sci 46:205–221

Reich PB, Tjoelker MG, Machado J-L, Oleksyn J (2006) Universal scaling of respiratory metabolism, size and nitrogen in plants. Nature 439:457–461

Reynolds JF, Thornley JHM (1982) A shoot: root partitioning model. Ann Bot 49:585–597

Ries L, Sisk TD (2004) A predictive model of edge effects. Ecology 85:2917–2926

Scheffer M et al (2006) Small habitat size and isolation can promote species richness: second-order effects on biodiversity in shallow lakes and ponds. Oikos 112:227–231

Schleppi P, Bucher-Wallin I, Hagedorn F, Koerner C (2012) Increased nitrate availability in the soil of a mixed mature temperate forest subjected to elevated CO_2 concentration (canopy FACE). Glob Change Biol 18:757–768

Sherratt TN, Wilkinson DM (2010) Big questions in ecology and evolution. Oxford University Press, New York

Spinnler D, Egli P, Körner C (2002) Four-year growth dynamics of beech-spruce model ecosystems under CO_2 enrichment on two different forest soils. Trees Struct Funct 16:423–436

Stöcklin J, Körner C (1999) Interactive effects of elevated CO_2, P availability and legume presence on calcareous grassland: results of a glasshouse experiment. Funct Ecol 13:200–209

Taneva L, Pippen JS, Schlesinger WH, Gonzalez-Meler MA (2006) The turnover of carbon pools contributing to soil CO_2 and soil respiration in a temperate forest exposed to elevated CO_2 concentration. Glob Change Biol 12:983–994

Treseder KK (2004) A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO_2 in field studies. New Phytol 164:347–355

Tricker PJ et al (2009) Water use of a bioenergy plantation increases in a future high CO2 world. Biomass Bioenergy 33:200–208

Vitousek PM, Sanford RL (1986) Nutrient cycling in moist tropical forest. Annu Rev Ecol Syst 17:137–167

Voelker SL, Muzika R-M, Guyette RP, Stambaugh MC (2006) Historical CO_2 growth enhancement declines with age in Quercus and Pinus. Ecol Monogr 76:549–564

Von Felten S, Hättenschwiler S, Saurer M, Siegwolf R (2007) Carbon allocation in shoots of alpine treeline conifers in a CO_2 enriched environment. Trees Struct Funct 21:283–294

Wang X, Taub DR (2010) Interactive effects of elevated carbon dioxide and environmental stresses on root mass fraction in plants: a meta-analytical synthesis using pairwise techniques. Oecologia 163:1–11

Wardlaw IF (1990) Tansley review no 27—the control of carbon partitioning in plants. New Phytol 116:341–381

Wittwer SH (1983) Rising atmospheric CO_2 and crop productivity. HortScience 18:667–673

Würth MKR, Winter K, Korner C (1998) Leaf carbohydrate responses to CO_2 enrichment at the top of a tropical forest. Oecologia 116:18–25

Zak DR, Pregitzer KS, King JS, Holmes WE (2000) Elevated atmospheric CO_2, fine roots and the response of soil microorganisms: a review and hypothesis. New Phytol 147:201–222