Plant and Soil **187:** 391–400, 1996.

The effects of elevated [CO_2] on plant-soil carbon below-ground: A summary and synthesis

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Key words: belowground respiration, ecosystem carbon balance, enhanced atmospheric [CO_2], root symbionts, root turnover, soil carbon accumulation

Abstract

We undertake a synthesis of the most relevant results from the presentations at the meeting "Plant-Soil Carbon Below-Ground: The Effects of Elevated CO_2" (Oxford-UK, September 1995), many of which are published in this Special Issue. Below-ground responses to elevated [CO_2] are important because the capacity of soils for long-term carbon sequestration. We draw the following conclusions: (i) several ecosystems exposed to elevated [CO_2] showed sustained increased CO_2 uptake at the plot level for many years. A few systems, however, showed complete down-regulation of net CO_2 uptake after several years of elevated [CO_2] exposure; (ii) under elevated [CO_2], a greater proportion of fixed carbon is generally allocated below-ground, potentially increasing the capacity of below-ground sinks; and (iii) some of the increased capacity of these sinks may lead to increased long-term soil carbon sequestration, although strong evidence is still lacking. We highlight the need for more soil studies to be undertaken within ongoing ecosystem-level experiments, and suggest that while some key experiments already established should be maintained to allow long term effects and feedbacks to take place, more research effort should be directed to mechanisms of soil organic matter stabilization.

Introduction

Considerable uncertainty remains as to whether the increasing anthropogenic CO_2 emitted to the atmosphere is sequestered temporarily in oceans and the terrestrial biosphere, or long-term in deep oceans and soils (Enting and Mansbridge, 1989; Francey et al., 1995). If the atmospheric and climatic consequences of future fossil fuel consumption scenarios are to be predicted with any confidence, it is crucial to establish the relationship between the Earth's different carbon sources and sinks. Because of the importance of this issue to policy making, a major research effort has been devoted to improving understanding of the global carbon cycle, and in particular, the coupling of the terrestrial biosphere with a changing atmosphere (Amthor, 1995; Houghton et al., 1995; Schimel et al., 1994; Siegenthaler and Sarmiento, 1993).

The largest stores of carbon in terrestrial ecosystems are in wood and soil, with the latter accounting for about two thirds of the total stored (Schimel et al., 1994). In this regard, the significance of soils is more than just their overall pool size; soils contain carbon fractions with the longest resident time relative to biomass, so that changes in these fractions would have the largest effects on the capacity of the terrestrial biosphere to sequester carbon in the long-term.

The purpose of this paper is to summarize and integrate the most relevant results from the presentations of the meeting "Plant-Soil Carbon Below-Ground: The Effects of Elevated [CO_2]" (Oxford-UK, September 1996). The meeting aimed to bring together current understanding of the effects of increasing atmospheric [CO_2] on the carbon fluxes entering the soil, the mechanisms of carbon transformation and ultimately, the

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formation of long-term Soil Organic Matter (SOM). References to the wider literature are to give context, or improve clarity. We conclude by highlighting a few major conclusions from the meeting, and suggesting areas where knowledge seems weakest - and hence where greater research effort should be focused.

Net CO_2 uptake and ecosystem carbon balance

Net photosynthesis (Pn) down-regulation at elevated $[CO_2]$ was first thought it would bring the net carbon uptake rate back to that of the ambient $[CO_2]$ level within months due to starch accumulation in leaves (Bazzaz, 1990; Stitt, 1991). Recent work carried out in field plots suggests nutrient limitation to be the primary cause of Pn down-regulation and that complete down-regulation at the leaf-level rarely occurs (Sage, 1994). However, changes in net ecosystem CO_2 uptake may also occur through changes in leaf area ratios and canopy Leaf Area Index (LAI).

Simplified and highly manipulated single-species systems have been key for understanding some of the mechanisms underlying Pn down-regulation. Gorissen (1996) found no biomass response to elevated $[CO_2]$ for ryegrass when growing at low nutrient availability, but a sustained 13% to 62% increased biomass when plants were well supplied with nutrients. Similarly, Steve Long (University of Essex, UK) reported that Pn down-regulation in wheat is tightly related to root nitrogen supply, and no down-regulation occurred in wheat grown at elevated $[CO_2]$ in FACE when given a high rate of nitrogen fertilizer. However, Rubisco activity and nitrogen concentration decreased in crops grown at low N availability. Thus, in natural systems which are commonly low in soil fertility, and hence are expected to be nitrogen limited at high $[CO_2]$ (due to an increased nitrogen demand by faster-growing plants and microbial N immobilization; Diaz et al., 1993), downward regulation of net ecosystem CO_2 uptake is expected to be common.

One of the most solid arguments as to whether the terrestrial vegetation will be able to sustain increased carbon uptake with increasing atmospheric $[CO_2]$ is provided by long-term field experiments in a variety of ecosystem types. Such studies, conducted in salt marsh, alpine pasture, Artic tundra, Mediterranean annual grassland, tallgrass prairie, chaparral and oak-woodland, found various degrees of increased biomass over several years of continuous CO_2 enrichment using Open-Top Chambers (OTC), Close-Top Chambers (CTP) or Free-Air CO_2 Enrichment (FACE) technology. In all these systems some degree of net ecosystem CO_2 uptake down-regulation occurred, but for some, complete down-regulation took place after only few years of exposure to elevated $[CO_2]$.

In the longest-running field experiment (eight years of elevated $[CO_2]$ exposure using OTC in a wetland community in Maryland, USA), Drake et al. (1996) showed a 30-100% increase in photosynthetic rate at the leaf-level and a 60% increase in net CO_2 uptake at canopy-level. Net ecosystem CO_2 uptake increase occurred even with some degree of leaf-level Pn down-regulation, i.e. a reduction of Rubisco and protein concentrations (see also Long and Drake, 1991). Similarly, after 5 years of continuous CO_2 enrichment using OTC, rates of photosynthesis of both C_3 and C_4 species in a tallgrass prairie remained higher in the elevated $[CO_2]$ treatments, though the increased net primary productivity has been attributed to alleviation of drought stress (Owensby et al., 1994). Likewise, in an alpine grassland, Diemer (1994) reported a 41% increase in CO_2 uptake at mid-season after 3 years of CO_2 enrichment, yet no above-ground biomass increase was observed and only a small below-ground biomass increase was detected (Körner et al., 1996). Contrary to the above results, an Arctic tundra site showed complete down-regulation after 3 years of elevated $[CO_2]$ exposure (Oechel et al., 1994).

The finding that more carbon was fixed in systems exposed to elevated $[CO_2]$ than could subsequently be accounted for in the biomass and soils was not a result unique to Körner's study; it was also observed in several other field studies. After exposing *Quercus alba* saplings to elevated $[CO_2]$ for four growing seasons, Richard Norby (Oak Ridge National Laboratory, USA) could balance the carbon budget in their ambient $[CO_2]$ OTC-plots, but estimated that 37% of the assimilated carbon could not be accounted for in their elevated $[CO_2]$ treatment. He pointed to the calculation of net CO_2 uptake and fine root respiration, and the omission of some below-ground sinks such as mycorrhizal respiration as the most likely causes of this discrepancy. Likewise, for an annual grassland exposed to elevated $[CO_2]$ for four years, an estimated 60% increase in carbon was assigned to root exudation, root turnover and root respiration; root biomass increased by about 30% in the elevated $[CO_2]$ OTC-plots (Bruce Hungate, University of California at Berkeley, USA).

In the light of the above results, we conclude that despite some degree of leaf-level Pn down-regulation there is strong evidence that some field system-plots exposed to elevated [CO_2] for a number of years can sustain increased net carbon uptake; other systems, however, complete down-regulation of net ecosystem CO_2 uptake occurred after few years of high [CO_2] exposure.

Below-ground carbon fluxes and sinks

As discussed above, increased net ecosystem CO_2 uptake is common for some ecosystem-plots exposed to elevated [CO_2], but the fate of the carbon among different pools has yet to be established. A growing body of information indicates that elevated [CO_2] increases the amount of carbon allocated below-ground compared with ambient levels (Gorissen, 1996; Ineson et al., 1996; Van Veen et al., 1991). This increased carbon flow to the belowground compartment could be driven by enhanced root exudation, root turnover, mycorrhizal development and N_2-fixation. However, while it is relatively easy to measure carbon input to the soil from above-ground litter, challenging methodological difficulties emerge when trying to measure below-ground inputs, e.g. root turnover or root exudation (Van de Geijn and Van Veen, 1993). The result is that not all the possible carbon fates can be measured precisely enough to balance the carbon budget of system-plots exposed to elevated [CO_2].

Despite some methodological difficulties, the use of the stable isotope ^{13}C and the radioactive isotope ^{14}C in several microcosm experiments provides reliable evidence that, under elevated [CO_2], more carbon is indeed being allocated below-ground. Gorissen (1996) found that, regardless of the total biomass response to elevated [CO_2], total net ^{14}C-CO_2 uptake increased by an average of 41%, and that carbon transferred to the roots and then to the soil increased between 31% and 35% in elevated [CO_2] treatments, when compared to ambient [CO_2]. Similarly, using the $\delta^{13}C$ differences found from growing C_3 plants on C_4 plant-derived soil, Ineson et al. (1996) demonstrated a three-fold increase in carbon input below-ground due to an increase of root biomass and root turnover.

Root biomass, phenology and turnover

In order to meet the increasing nutrient demands of faster growing plants, rising atmospheric [CO_2] is expected to increase the carbon allocated to building larger root systems. To date, however, the measured root:shoot biomass ratio in different elevated [CO_2] experiments has been shown to either increase, decrease, and to show no change at all (Fitter et al., 1996; Gregory et al., 1996; Ineson et al., 1996; Rogers et al., 1996). The conclusion is that an absolute increase of root biomass is fairly common when plants show a positive biomass response to elevated [CO_2], but no consistent pattern has been found with respect to the root:shoot biomass ratio, at least, in natural ecosystems. A mechanistic hypothesis to explain the lack of general trends has been discussed elsewhere (Luo et al., 1994).

Not only do root biomass measurements show an inconsistent response to elevated (CO_2), but they also tell little about the flux of carbon below-ground, and consequently little about the capacities of the carbon sinks. The measurement of root turnover does however, account for an important part of the carbon flowing down to the roots, including changes both in pool size and root demography; root turnover may in fact be one of the most important mechanisms of carbon transfer to the soil (Van Veen et al., 1991), yet we still know very little about how elevated [CO_2] may change its rate and phenology.

There is evidence that turnover increases with increased allocation to root systems when plants are grown under elevated [CO_2], at least in grasslands and forest (Fitter et al., 1996). In two different grassland types in northern England biomass was increased under elevated [CO_2] and in each type both root birth and death rates increased, resulting in more rapid throughput of carbon. In one of these grasslands root half-lives were shorter under elevated than ambient [CO_2], so that turnover was increased disproportionately. In wheat, in contrast, although root biomass was substantially increased, there was no increase in turnover because root mortality in wheat does not occur until the crop is well developed, but there was a marked change in the spatial and temporal pattern of root development, with plants at elevated [CO_2] having greater root growth in upper soil layers, and reduced and delayed growth at depth.

Other examples were presented by Alastair Fitter (York University, UK) which illustrated that root turnover does not respond consistently to enhanced [CO_2]; nevertheless, the commonest result is faster root turnover. In four experiments on trees, increased root turnover at elevated [CO_2] was observed in three while one showed a decrease. In four experiments on grassland systems, increased root turnover was observed in three, and one showed no change. Finally, no difference in root turnover was found for a wheat crop growing at elevated [CO_2].

Decomposition and soil carbon storage depend on several factors, but root phenology and depth distribution can be important in governing long-term carbon sequestration (Fisher et al., 1994). Shifts in spatio-temporal patterns of root growth in response to elevated [CO_2] may affect both plant performance and carbon residence time in soil, if for example shallower rooting is a widespread response (Fitter et al., 1996; Roger et al., 1996).

Root exudation

Although a relatively minor pathway for transferring carbon to soils, relative to fine root death, the nature of the exudates may be more important for ecosystem function than their overall quantity (Cardon, 1996). For instance, exudation of acid phosphatase may constitute a very small portion of the total carbon lost to the rhizosphere, yet the function of this enzyme may be extremely important in releasing phosphorus from phosphate ester in SOM, thereby compensating in part for phosphorus limitation. Cardon showed a 220% increase of phosphatase activity at the stand-level for a California annual grassland exposed to elevated [CO_2] during one growing season. The increase was driven by increased root biomass and not because of increased root activity. Increase of total acid phosphatase activity was also reported by Dhillion and Roy (1996) for *Bromus madritensis* monocultures following one growing season of elevated [CO_2] in a mesocosm, and by Gifford et al. (1996) for *Danthonia richardsonii* grass in Australia.

In addition to acid phosphatase, increased exudation of organic acids (expressed per gram of root) were reported for *Eucalyptus rossii* in SE Australia (Damian Barret, CSIRO, Australia). Organic acids, mainly citrate, can cause the release of inorganic phosphorus from aluminum and iron complexes in soils, which (akin to the effect of the enzyme discussed above) may have a positive feedback on plant growth through increased phosphorus availability. Increased exudation of both phosphatase and organic acids could be an important driver of the ecosystem long-term response to elevated [CO_2] in phosphorus-limited ecosystems.

Root symbionts: Mycorrhiza and N_2-fixing organisms

Root symbionts such as mycorrhiza and nodulated roots are potentially strong carbon sinks for the enhanced carbon fixed at elevated [CO_2]. Both root symbiont types also enhance nutrient availability so that the predicted decrease of the soil nutrient status in high atmospheric [CO_2] environments could be partially ameliorated (Díaz, 1996). An increase in root symbiont activity at elevated [CO_2] could therefore result in a positive feedback on net CO_2 uptake and further strengthen the carbon sink below-ground. In addition to accounting for possibly 15% to 20% of the NPP in some natural systems (Melanie Jones, Okanagan University, Canada), mycorrhizal biomass could also enhance the below-ground carbon sink through increased root turnover rate.

About half of the studies that have reported data on either ectomycorrhiza or arbuscular mycorrhizae (AM) infection have found higher infection rates at high [CO_2], while the other half found no change (see also O'Neill, 1994). These, and other studies (Díaz, 1996), conclude that no consistent pattern emerges. Diaz also showed that increased mycorrhizal activity at high [CO_2] (when it occurs) was mostly due to increased root biomass with the consequent increased mycorrhizal infection, rather than a change of the infection per unit root production (biomass or length).

Mycorrhizal infection rates, however, may tell very little about the total carbon invested in mycorrhizal associations. Instead, Jones suggested measuring the mantle thickness of ectomycorrhizae, and the number of vesicles and the external hyphae production of AM. Endomycorrhizal biomass measurement techniques are not yet available.

Finally, changes in mycorrhizal community composition may have even stronger effects on carbon fluxes than changes in infection rates or changes in the physiology of species because different mycorrhizal species have distinct carbon transfer rates (Díaz, 1996). Furthermore, changes in the competitive ability of symbiotic plant species versus non-symbiotic species may bring larger changes in whole ecosystem function than those due to changes in infection rates or mycorrhizal function.

An increase in N_2-fixation in root-nodulated plants would increase both the below-ground carbon sink and nitrogen availability. However, neither the efficiency nor the cost of the N_2-fixation process seems to be directly affected by elevated [CO_2]; the effects at the plant level are mainly due to changes in root biomass and hence, number of nodules per plant and/or changes in the individual weight of the nodules (Soussana and Hartwig, 1996).

In Switzerland, FACE experiments with fertilized *Trifolium repens* showed no changes in leaf nitrogen and an increase of 15-35% in total plant nitrogen at elevated [CO_2]. By taking advantage of the diffenences in $\delta^{15}N$ values between nitrogenous compounds containing N_2 fixed from the atmosphere (as opposed to nitrogen from the soil), Soussana and Hartwig (1996) were able to determine that most of the increased total nitrogen was due to an increase in N_2-fixation.

It is still debatable whether increased N availability by N_2 fixation would lead unquestionably to increased carbon uptake. Litter from legumes grown under elevated [CO_2] has consistently shown a lower C:N ratio than in non-legumes (per unit biomass). This adds more N to the soil system and speeds up mineralization rates, both of which could lead to increased plant biomass and/or faster carbon and nitrogen turnover times. For instance, Clark et al. (1995) have shown a faster carbon turnover by *Lolium perenne* and *T. repens* grassland when exposed to elevated [CO_2], but no changes in pool size were found. Alternatively, increased nitrogen availability provided by the higher performance of legumes at elevated [CO_2] could be used by non-legume plants resulting in an overall increased stand net primary productivity; depending on the abundance of legume species, terrestrial vegetation could therefore vary greatly in its response to elevated [CO_2]. It is evident that increased attention must be devoted to understanding whether elevated [CO_2] changes the coupling of the carbon and nitrogen cycles (e.g. Berntson and Bazzaz, 1996) in a variety of scenarios including those with and without N_2-fixing organisms.

In conclusion, while it is not clear whether increased symbiont activity will lead to enhanced NPP, in general mycorrhizal and nodulated plant species are stimulated by high [CO_2] to a greater extent than are non-symbiotic species (Díaz, 1996). Any beneficial effect of enhanced symbiotic activity at elevated [CO_2] is therefore more likely to be evident in communities with a high abundance of legumes. However, long-term changes in species composition due to altered competitive ability (legumes versus non-legumes) under elevated [CO_2], may cause changes in community composition with important functional changes at the ecosystem level.

Root and soil respiration

There is no evidence for a direct effect of elevated [CO_2] on below-ground respiration (roots and microbes), but plant-mediated effects are expected to be important because of the predicted increases in root biomass and rhizodeposition (Lambers et al., 1996). Indeed, enhanced soil respiration is a common response to increased elevated [CO_2] (Drake et al., 1996; Gorissen, 1996), although the distinction between root and microbial respiration is rarely reported. The separation between these two components, and therefore between the substrates that are respired, has major implications for long-term carbon storage. Gorissen (1996) used ^{14}C-CO_2 to trace the fate of carbon in *Pseudotsuga menziessi* saplings, *Lolium perenne* and *Triticum aestivum* growing at ambient and elevated [CO_2] treatments in different microcosm experiments. In all experiments he found an increase from 13% to 16% in soil respiration (root plus microbial) at elevated [CO_2], with respect to the ambient [CO_2] treatment.

While elevated [CO_2] quite consistently suppresses leaf respiration, results from greenhouse and laboratory experiments show no clear pattern for root respiration under such conditions. However, a great deal of variation can be explained by the interaction between elevated [CO_2] and nutrient availability. When plants are grown at optimum nutrient and water supply, elevated [CO_2] affects neither carbon partitioning nor root respiration per unit root mass (although the total respiration may increase because of larger plants) (Lambers et al., 1996). In natural systems, however, with low nutrient availability, root respiration will remain equal or increase under elevated [CO_2] according to the relative effect on biomass partitioning between root and shoot, and total root biomass production.

The non-root, non-symbiont soil respiration comes from microbial biomass and its activity, and increases in these under elevated [CO_2] have been reported (Dhillion and Roy, 1996; Clenton Owensby, Kansas State University, USA).

Elevated [CO_2] and soil carbon storage

Changes in the soil carbon pools due to the effects of elevated [CO_2] from only a few years of exposure are expected to be small and difficult to detect. Even for the scenarios with the largest enhanced net CO_2 uptake at elevated [CO_2], changes of the soil carbon content would not be larger than a fraction of a percent (Amthor, 1995). In support of this, Hungate et al. (1996) found no consistent changes in soil carbon content in an annual grassland exposed to elevated [CO_2] for four years. They calculated the rates of incorporation of new carbon into the soil by using the depleted $\delta^{13}C$ signal of the bottle CO_2, and determined that the chance to detect a statistically significant change in the soil carbon content under realistic scenarios of increased net CO_2 uptake at elevated $[CO_2]$ was only 9% after 3.3 years of fumigation.

Some field studies have however shown a trend towards increasing soil carbon storage in elevated $[CO_2]$ plots, yet it was not statistically significant for some. Among the field studies are a wetland in Maryland (USA) after 6 years of CO_2 fumigation (Drake et al., 1996), a Kansas (USA) tallgrass prairie after 5 years of CO_2 fumigation (Clenton Owensby, Kansas State University), and the Arizona FACE (USA) after 3 years of cotton production (Leavitt et al., 1994).

One solution to detecting a small change in a large soil carbon pool is to use isotope tracers to quantify small amounts of carbon deposition. ^{14}C-CO_2 has been extensively used to study plant-soil carbon fluxes, but the use of the stable ^{13}C is becoming an important tool for understanding carbon dynamics in field studies (Ineson et al., 1996; Leavitt et al., 1996). More specifically, the technique of growing C_3 plants in soil derived from C_4 vegetation allows the CO_2 evolving from plant-derived substrate to be separated from that evolving from older SOM (Cardon, 1996; Ineson et al., 1996), despite some problems due to microbial fractionation (Mary et al., 1992).

There are however other methodologies available to tackle the intrinsic difficulty of detecting changes in the soil carbon pool in short term CO_2 fumigation experiments, such as SOM physical or chemical fractionation techniques (Cambardella and Elliott,1994; Elliott and Cambardella, 1991). To some extent these techniques allow old SOM to be separated from more recently deposited material, the latter having been influenced by the experimental conditions. Soil laboratory incubations provide another good approach (Eldor Paul, Michigan State University, USA), in which microbes fractionate the different soil carbon pools starting with the more recently deposited carbon (highly labile) and continuing with the more recalcitrant fractions.

Direct and indirect effects of elevated $[CO_2]$ may alter microbial substrate preference and thus the quality of the carbon left following their activity (Cardon, 1996). Shorter turnover times at elevated $[CO_2]$ are also possible, which means that more carbon would cycle through the plant-soil system, although this would not necessarily result in an increase of net carbon storage.

Long-term feedbacks

Any relevant contribution terrestrial ecosystems may make in response to predicted changes in atmospheric composition must act over decade to centuries time frame. Short-term responses (< 10 year) derived from field experiments may be of limited value in predicting long-term responses in which biogeochemical feedbacks and interactions with stress factors may result in new scenarios of resource balance, and the composition of plant species and soil microbial communities (Field et al., 1992; Sage, 1996).

Berntson and Bazzaz (1996) provided an excellent conceptual model of integrated plant-soil interactions to account for negative and positive feedbacks affecting plant growth responses to elevated $[CO_2]$ over a decadal time-frame. Primary negative feedbacks are related to decreasing nutrient availability to plants, such as increased C:N ratios (and the subsequent reduced mineralization rates), increased microbial immobilization and increased storage of nutrients in plant material due to increases in NPP. Positive feedbacks included increased mineralization due to increased microbial activity and changes in root and mycorrhizae traits which could allow higher nutrient uptake capacity. Thus, an integrated system-level study approach is needed in order to account for simultaneous positive and negative feedbacks which would allow to assess the net direction of those feedbacks (Bernstson and Bazzaz, 1996).

Long-term feedbacks may however be far more complex than the outline given above, often due to changes in soil biota. One example is the possible ecosystem change brought about by structural changes of the soil food-web which may occur through altered carbon inputs from plants. There is also evidence for a shift in the relative abundance of species of ectomycorrhizal fungi from mutualistic to more opportunistic/parasitic interactions when plants were exposed to elevated $[CO_2]$ (Díaz, 1996). Others have found changes in the microbial community composition and/or the relative activities of bacteria versus fungi (Canadell, unpublished). Changes in the below-ground food web structure may have long-term implications for litter decomposition, while changes in microbial activity have been shown by an increase dehydrogenase activity in *Bromus madritensis* monocultures growing at elevated $[CO_2]$, with an associated increased SOM decomposition rate (Dhillion and Roy, 1996).

A change in the rate of litter decomposition will have major implications for nutrient availability, and thus for net primary productivity response to elevated [CO_2] (Field et al., 1992). Gorissen (1996) found decomposition rates decreased by more than 30% in 64-day laboratory incubations of roots which had been grown at high [CO_2] and low nitrogen availability. This decreased decomposition could be due to an increased C:N ratio but ambient and elevated [CO_2] treatments had no significant differences in initial C:N, and only a small difference in lignin content. While ecosystem model predictions are assuming an increased C:N ratio of the various carbon pools, field experiments have shown very little effect of elevated [CO_2] on litter quality and decomposition (Koch and Mooney, 1996).

Synthesizing our new knowledge into models

The application of models of terrestrial carbon cycling and, in particular, to the controls on soil carbon turnover and accumulation is an important step. Paustian et al. (1996) used the CENTURY model to evaluate the interactions between climate change (including temperature and precipitation), CO_2 fertilization and management in influencing soil carbon levels in three agroecosystems: a conventional winter wheat-summer fallow rotation, a wheat-corn-fallow rotation, and continuous cropping with wheat. The model analyses showed that management practice was more important than any aspect of climate change or [CO_2] in controlling soil carbon levels. The wheat-fallow rotation resulted either in losses of soil carbon or minimal gains depending on the combination of climate and [CO_2]. The other two management practices (which both reduce summer fallowing) resulted in increases in soil carbon with greater increases occurring under climate change and CO_2 fertilization. The analysis illustrates the importance of considering management practices and changes in them - when attempting to project the effects of [CO_2] change on terrestrial carbon storage.

A model useful for understanding the conditions under which carbon will accumulate in terrestrial ecosystems when atmospheric [CO_2] is increasing was presented by Yiqi Luo (Desert Research Institute, USA). He proposed that ecosystem photosynthesis and respiration increase differentially as [CO_2] increases, and that the lag in the increase in respiration allows carbon to accumulate. The increase in carbon input to ecosystems from photosynthesis responding to high [CO_2] is essentially instantaneous. As pools of carbon increase, plant and microbial respiration will also increase, but there is a lag because much of the carbon is allocated to carbon pools with long residence times (e.g. wood or recalcitrant soil carbon). If the amount of carbon allocated to different pools and the residence times of those pools are known, then a mean ecosystem carbon residence time can be calculated and used to quantify the time delay in the response of respiration. The model was applied to several case studies. A particularly important conclusion was that ecosystems respond very differently to a gradual versus a step increase in [CO_2]. This has major implications for the design and interpretation of experiments.

Parton (Colorado State University, USA) showed the value of model intercomparison studies for advancing our understanding of the processes controlling carbon accumulation in ecosystems. He described some of the results of the Vegetation/Ecosystem Modelling and Analysis Project (VEMAP Members, 1995). When three biogeochemistry models were run for contemporary climate and CO_2 they produced similar results in terms of NPP and ecosystem carbon storage. Under elevated [CO_2] and climate change, however, the results diverged significantly, particularly with regard to soil carbon. This indicates that we still do not fully understand the controls on key ecosystem processes, especially under novel conditions of atmospheric CO_2 and climate. Parton discussed a new effort to improve links between the development of models and the findings from experiments. The CO_2 Model/Experiments Activity for Improved Links (CMEAL) is comparing the responses to elevated [CO_2] of eight models and will also undertake a comprehensive analysis of experimental results in order to better understand the differences among models and lead to a better mechanistic understanding of the responses of ecosystems.

Finally a global version of CQUESTN was used to investigate past and future carbon sequestration in terrestrial ecosystems as influenced by increases in atmospheric [CO_2], temperature and N-deposition (Gifford et al., 1996). Using reasonable estimates of global nitrogen and carbon pools, turnover times and fluxes, as well as credible mechanisms of ecosystem response, it is concluded that increases in CO_2, temperature and N-deposition could account for a net terrestrial sink for carbon of 3-4 Gt yr^{-1}. With somewhat less conservative assumptions, the estimated sink could be as great as 4-5 Gt yr^{-1}. The latter number significantly exceeds the magnitude of the "missing sink" derived from models that do not include the effects of [CO_2], temperature and nitrogen on terrestrial systems. One noteworthy conclusion from the modeling was that increasing temperature would increase ecosystem carbon storage. This is because the nitrogen released as a result of temperature-enhanced mineralization was taken up by plants and redisitributed from the soil where C:N ratios are low into vegetation where C:N ratios are high. This agrees with predictions made by other models (McGuire et al., 1995) and needs to be further investigated experimentally.

Conclusions

Understanding below-ground responses to elevated [CO_2] is important because the soils potential capacity for long-term carbon sequestration. From the above information we draw the following conclusions:

(i) several ecosystems exposed to elevated [CO_2] showed sustained increased CO_2 uptake at the plot level for many years. A few others, however, showed complete down-regulation of net CO_2 uptake after several years of elevated [CO_2] exposure;

(ii) under elevated [CO_2], a greater proportion of fixed carbon is generally allocated below-ground, potentially increasing the capacity of below-ground sinks; and

(iii) some of the increased capacity of these sinks may lead to increased long-term soil carbon sequestration, although strong evidence is still lacking.

As the reader will have inferred from this paper, there is substantially more understanding about the effects of enhanced [CO_2] on above- than on below-ground processes. This is increasingly the case as we try to be more precise about one of the key issues, SOM stabilization: irrespective of the pathway through which carbon enters the soil, the final question posed is whether the carbon will be respired back to the atmosphere in a relatively short time, or remain in the soil and become (in part) long-term SOM.

SOM storage is not however, only, affected by [CO_2]. For those soils of the world under intensive management, the effect of elevated [CO_2] on SOM stabilization may be a second order issue; tillage, irrigation, and fertilization will dominate. Climate change will also be an important factor (particularly where it brings about a change in land use or management), and, as with elevated [CO_2], it will affect both highly managed and unmanaged systems.

Future research directions

If the terrestrial biosphere is to sequester more carbon in a high [CO_2] world, one of the most important places to look for changes in carbon content is the soil; measurements of plant-mediated processes (e.g. photosynthesis, or root biomass and turnover) cannot alone give an indication of the carbon being stored below-ground. In describing many of the ecosystem-level CO_2 experiments which currently exist, the meeting highlighted that they are often oriented more towards plant responses with less analysis conducted on the response of the soil components. Several such experiments could however provide ideal opportunities for below-ground studies, which both increase the cost-effectiveness of the experiments and help to explain observed results. This is wholly congruent with the notion that more soil research is needed.

More research should be undertaken on rhizosphere processes; and, given the importance of the interaction with nutrition, especially on the poorly understood role of symbionts. Effort should also be directed towards methods for quantifying SOM fractions and their functional role; physical methods of pool separation are coming into increasing favour, although a limited number of the more classical chemical methods are also being applied effectively in global change work. Approaches that apply chemical characterization of physically separated fractions show promise and should be further developed.

The most important message however is one of time scale. The relatively long SOM turnover time is likely to preclude the use of many short-term experiments for the analysis of SOM dynamics (although with the application of methods able to discern the more rapidly turning over SOM pools, they may be of more value than previously thought). We should therefore continue to run selected field experiments for longer than perhaps originally envisaged (e.g. > 10 years) so that we can increase the likelihood of direct observation of increased soil carbon levels, and account for feedbacks and interactions with other stresses over longer periods. There is also a need for more process-based experiments aimed at elucidating SOM stabilization mechanisms.

Finally, more long-term measurements of net ecosystem CO_2 uptake are necessary in order to study seasonal patterns and annual inter-variability of system responses to elevated [CO_2].

Acknowledgements

We wish to thank Sabrina Sonntag, Hal Mooney, Bernard Tinker and Peter Gregory for helpful comments on the manuscript. We also thank all the participants of the Oxford meeting, particularly Christian Körner and Fakhri Bazzaz, who made sure that this manuscript was clear and accurate in reproducing the main results of the meeting.

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Section editor: H Lambers