

Review and synthesis of the effects of elevated atmospheric CO₂ on soil processes: No changes in pools, but increased fluxes and accelerated cycles

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ABSTRACT

Atmospheric change encompassing a rising carbon dioxide (CO₂) concentration is one component of Global Change that affects various ecosystem processes and functions. The effects of elevated CO₂ (eCO₂) on belowground processes are incompletely understood due to complex interactions among various ecosystem fluxes and components such as net primary productivity, carbon (C) inputs to soil, and the living and dead soil C and nutrient pools. Here we summarize the literature on the impacts of eCO₂ on 1) cycling of C and nitrogen (N), 2) microbial growth and enzyme activities, 3) turnover of soil organic matter (SOM) and induced priming effects including N mobilization/immobilization processes, and 4) associated nutrient mobilization from organic sources, 5) water budget with consequences for soil moisture, 6) formation and leaching of pedogenic carbonates, as well as 7) mobilization of nutrients and nonessential elements through accelerated weathering. We show that all effects in soil are indirect: they are mediated by plants through increased net primary production and C inputs by roots that foster intensive competition between plants and microorganisms for nutrients. Higher belowground C input from plants under eCO₂ is compensated by faster C turnover due to accelerated microbial growth, metabolism and respiration, higher enzymatic activities, and priming of soil C, N and P pools. We compare the effects of eCO₂ on pool size and associated fluxes in: soil C stocks vs. belowground C input, microbial biomass vs. CO₂ soil efflux vs. various microbial activities and functions, dissolved organic matter content vs. its production, nutrient stocks vs. fluxes etc. Based on these comparisons, we generalize that eCO₂ will have little impacts on pool size but will strongly accelerate the fluxes in biologically active and stable pools and consequently will accelerate biogeochemical cycles of C, nutrients and nonessential elements.

1. Introduction

1.1. CO₂ concentration in the atmosphere

John Tyndall (1859, 1872) recognized CO₂ as a greenhouse gas and Svante Arrhenius (1896) predicted its potential for global warming. This emerging concern about the effects of atmospheric CO₂ and its direct relationship to the global temperature has been verified by direct observations (Fig. 1) and by predictions based on global climate models (IPCC, 2014). Using ice core data on stable C and oxygen isotopes, a very close connection between atmospheric CO₂ and global

temperature has been shown for the last 800 kYears (Barnola et al., 1991; Petit et al., 1999; Hansen et al., 2013).

Over the millennia, the atmospheric CO₂ concentration remained below 300 ppm and varied over the last 800 kYears between ~180 ppm during the ice ages and ~280 ppm during the warm (interglacial) periods (Ganopolski et al., 2016) (Fig. 1). This was also the case during the last glaciation and the entire Holocene, but not during the Anthropocene.¹ During the Anthropocene the atmospheric CO₂ concentration started to increase in the last 150–200 years and this increase had accelerated over the past 30–50 years. 2013 was the first year in human history in which the CO₂ concentration reached 400 ppm, and

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¹ The Anthropocene is an epoch dating from the commencement of significant human impact on the Earth's geology and ecosystems, including but not limited to anthropogenic climate change. There is no unified opinion about the start of Anthropocene, but the main suggestions range between 1610 and 1964 (Crutzen, 2002, 2010; Lewis and Maslin, 2015). An early concept for the Anthropocene was the Noosphere by Vladimir Vernadsky (Lectures in Sorbonne, 1922–1923) as “scientific thought as a geological force” (Vernadsky, 1945) and was introduced as a term by Édouard Le Roy and Pierre Teilhard de Chardin in 1926.

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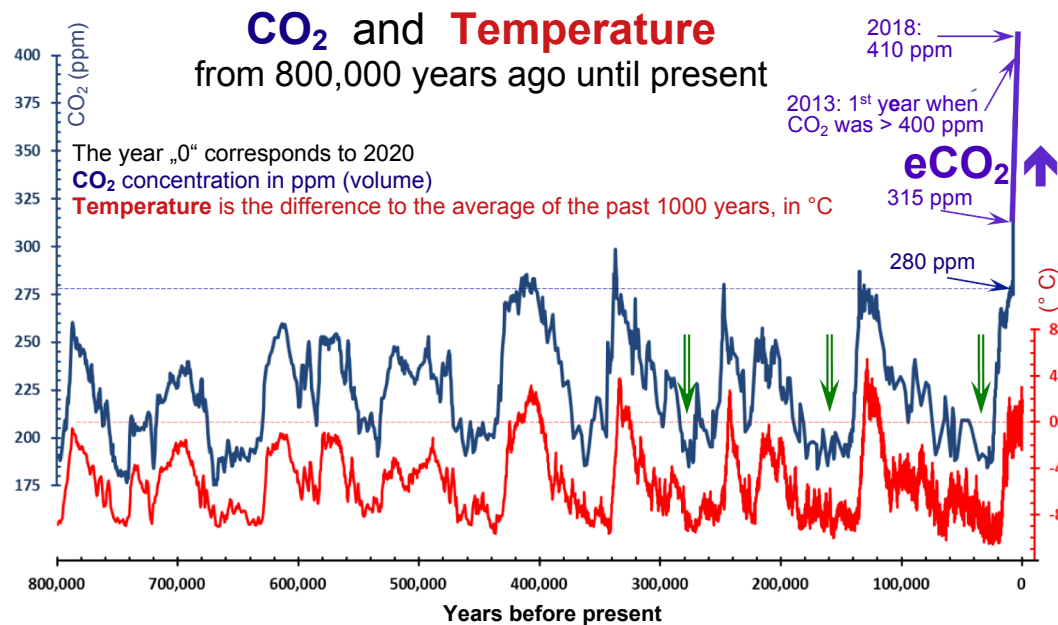


Fig. 1. CO₂ concentration in the atmosphere and temperature over the last 800 kYears. (from: <https://clas-pages.uncc.edu/mesas/news/>The figure is partly created by B. Magi, modified). eCO₂ ↑ represents “elevated CO₂”: the increase of CO₂ in the atmosphere compared to the preindustrial period (< 280 ppm). The green double arrows show the three last ice ages. The data of CO₂ measurements from the Mauna Loa (started 1958, ~315 ppm; Keeling et al., 1976) are presented in violet. Compiled from: Hansen et al. (2013), Ice core records from Antarctica: www.ncdc.noaa.gov/paleo/icecore/antarctica/domec/domec_epica_data.html. Current CO₂ measurements from NOAA: www.esrl.noaa.gov/gmd/ccgg/trends/. Current temperature from NASA: data.giss.nasa.gov/gistemp/graphs_v3/.

Table 1

Advantages and shortcomings of four main approaches to investigate effects of elevated CO₂ concentration in the atmosphere on processes in the plant-soil system.

Approaches	Advantages	Shortcomings ^a
Natural CO ₂ springs	<ul style="list-style-type: none"> - Natural CO₂ source - No costs 	<ul style="list-style-type: none"> - Few sites around the world - Azonal vegetation - Very fast CO₂ dilution resulting in variable concentrations and gradients - Toxic gases (H₂S, CO, SO₂) - Extreme soil conditions: high salinity, high soil temperature
Solardomes	<ul style="list-style-type: none"> - High CO₂ enrichment is possible - CO₂ with strongly shifted δ¹³C 	<ul style="list-style-type: none"> - Small scale (no upscaling) - No ecosystem processes - Mainly short-term studies - Lower solar radiation - Higher air temperature and humidity - Absence of wind turbulence - Ratio of diffuse/direct sunlight increased - More/fewer pest diseases
Open Top Chambers	<ul style="list-style-type: none"> - High CO₂ enrichment is possible - CO₂ with strongly shifted δ¹³C - “Low” costs - Nearly natural precipitation 	<ul style="list-style-type: none"> - Small scale (no upscaling) - No ecosystem processes - Mainly short-term studies - Lower solar radiation - Higher air temperature and humidity - Very low wind turbulence - Ratio of diffuse/direct sunlight increased - Higher/lower pest diseases
FACE experiments	<ul style="list-style-type: none"> - Studies of ecosystem processes - Natural precipitation & temperature - Low disturbance - Long-term studies - Medium scale - Natural energy balance and gas exchange - CO₂ with shifted δ¹³C to trace C sources in pools and fluxes 	<ul style="list-style-type: none"> - High CO₂ enrichment is impossible - No nighttime increase in CO₂** - Higher soil moisture - High costs of long-term CO₂ maintenance

**Some FACE experiments are fumigated at night.

^a Shortcomings are presented compared to natural conditions: ambient CO₂ concentration (380–400 ppm) without any equipment for CO₂ supply.

continues an unprecedented increase. The current level of atmospheric CO₂ has now permanently surpassed 410 ppm (<https://www.co2.earth/>), a level not seen for millions of years (Petit et al. 1999) (Fig. 1). We therefore need to better understand how elevated CO₂ in the atmosphere will affect processes and pools in ecosystems, particularly the large soil C pool.

Soil – as a fundamental part of every terrestrial ecosystem – is a critical component affecting the global C cycle and is the largest terrestrial C pool. This calls for understanding of the effects of rising atmospheric CO₂ on the biogeochemical processes and soil C pools. Most previous reviews on the effects of elevated atmospheric CO₂ (eCO₂) focused on the aboveground response of plants (Ainsworth and Long,

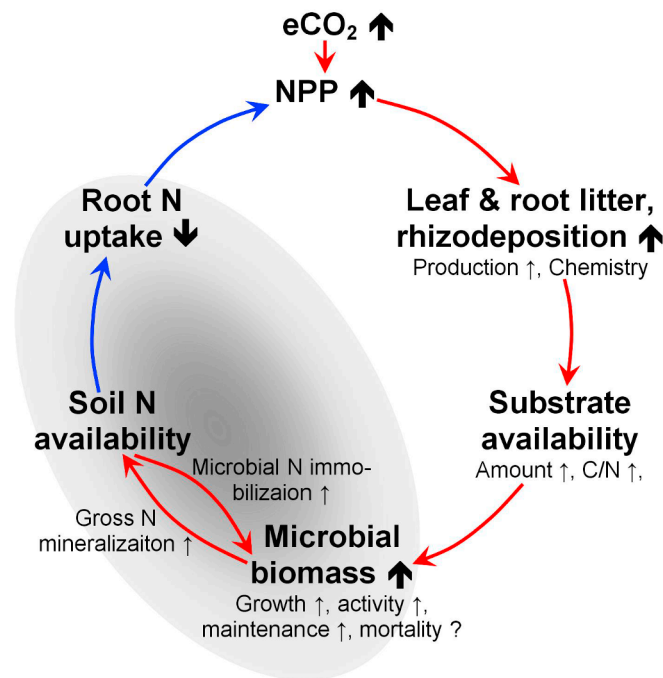


Fig. 2. Interactions between plant and microbial activities, and N availability under elevated CO_2 . (Zak et al. 2000, modified). Tight interactions between roots (release more rhizodeposits) and microorganisms (N immobilization at higher available C) lead to strong competition for N (gray area). eCO_2 ↑ represents the increase of atmospheric CO_2 – elevated CO_2 . Root N uptake (↓) decreases per produced plant biomass. The arrows reflect the increase (↑ ↑) or decrease (↓ ↓) of the respective pool, process intensity, or activity. Red and blue long arrows show the positive or negative effects (Compiled based on Feng et al., 2015; Phillips et al., 2012; Paterson et al., 1997; Hu et al., 2001; Zak et al. 2000; Dieleman et al., 2012; Liang et al., 2016; Rütting, 2017).

2005; Curtis and Wang, 1998; Kimball et al., 2002; Long et al., 2004). Only a few reviews or meta-analyses addressed individual belowground processes: root morphology, litter input by plants, rhizodeposition, N_2 fixation, mycorrhiza development and microbial composition (Paterson et al., 2007; Zak et al., 2000; Treseder and Allen, 2000; van Groenigen et al. 2006; Reich et al. 2006; Terrer et al., 2016). Importantly, the interdependence of individual processes as well as consequences for the processes and pools were not presented. This is the main aim of this review, with a focus on soil-plant-microbial interactions and consequences for the pools and fluxes of C, nutrients and water in soil.

1.2. Approaches to investigate effects of elevated CO_2 concentration on soil processes

Generally, two methodological approaches are used to evaluate eCO_2 effects. The first group involves controlled conditions, e.g. leaf chambers and climate chambers, where high CO_2 concentrations (up to few percent) are compared to the ambient level of 350–400 ppm. These approaches focus on investigating metabolic and physiological mechanisms at the level of a few leaves or individual plants and reflect the physiological potential for response of plants to eCO_2 . Accordingly, plant community responses and belowground processes are neglected in most of these studies.

The second group of methods considers multiple plants grown on field plots *in situ*. This group includes (Table 1): Natural CO_2 Springs, Solardomes, Open Top Chambers (OTC), and Free Air Carbon Dioxide Enrichment (FACE) experiments. Here, we highlight the advantages and shortcomings of these approaches (Table 1). For more details, see the extended reviews (McLeod and Long, 1999; Amthor, 2001; Norby and Zak, 2011). The most relevant approach to assess the effects of

eCO_2 on soil processes and at the ecosystem scale are FACE experiments: they have the lowest climate disturbance (heating, wind speed and turbulence, air humidity, soil moisture, etc.) and the soil remains an unaltered part of the ecosystem (Table 1). Therefore, this review is based solely on the FACE experiments.

1.3. Hypotheses

Considering the whole ecosystem (plants-soil-microorganisms) and based on the classical Le-Chatelier's principle ('Any change in status quo prompts an opposing reaction in the responding system'), one might hypothesize that increased atmospheric CO_2 concentration will lead to the maximal changes aboveground. Since leaves are the first plant organ affected by eCO_2 , photosynthesis and net primary productivity will experience initial effects that are expected maximal compared to other processes and pools in the ecosystems. The eCO_2 effects presumably decrease from the level of leaves to shoots, to roots, to mycorrhiza, to rhizosphere microorganisms, to non-rhizosphere microorganisms, and finally to SOM (see Fig. 1 in Bahn et al., 2010). This hypothesis, however, based on Le-Chatelier's principle, does not consider the interactions between the ecosystem components and associated limitations: eCO_2 will more strongly limit resources from soil – mainly nutrients. Accordingly, considering the shift in resource limitations from aboveground (atmospheric CO_2 concentration) to belowground (nutrients), we hypothesize that an increase in atmospheric CO_2 will intensify the full range of processes in soil to overcome nutrient limitation. More specifically, nutrient mobilization in soil will be intensified 1) by biotic processes: either microbial turnover, or extracellular enzyme activities catalyzing the decomposition of SOM and litter, thereby releasing nutrients (e.g. by priming effects); and 2) by biotic-abiotic interactions – mainly biochemical weathering, e.g. by more acidic agents released by roots and by microorganisms (both as biotic agents).

Based on this hypothesis specific for C and nutrients and considering that the increased inflows are compensated by increased outflows in each pool, we hypothesize that the increase of fluxes under eCO_2 will generally be much higher than the increase of the pool sizes.

2. Effects of elevated atmospheric CO_2 on soil processes

2.1. Direct and indirect effects of elevated atmospheric CO_2

All effects (including the effects of eCO_2 concentration on soil-plant-microbial interactions) can theoretically be direct or indirect. The general assumption is that direct effects are stronger than indirect ones. This, however, is not always the case for soils. Evaluating the direct effects of eCO_2 on soil processes requires comparing the CO_2 concentrations in the atmosphere versus soil. The latter is usually one or two orders of magnitude higher (5000 to 30,000 ppm, e.g. Andrews and Schlesinger, 2001; Lin et al., 2018) than that in the atmosphere and strongly increases with depth. Also, the variation in the soil CO_2 concentration is far higher than that in the atmosphere. Consequently, "small" atmospheric increase of "just" 100–200 ppm over the past century does not directly impact the CO_2 concentration in the soil. Even the CO_2 gradient between soil and atmosphere will likely remain unaffected. Therefore, the eCO_2 concentration in the atmosphere, which is expected to increase up to an additional ~150 (RCP4.5 scenario) to 300–600 ppm (RCP6.0 scenario) by 2100 (IPCC, 2014), will likely not affect any soil processes directly. This makes indirect effects (root and microbial respiration, slightly higher soil moisture) much more important for soils. However, investigating such indirect effects is much more difficult because they involve various multilevel interactions (Reich et al., 2006; Fatichi et al., 2016): between the pools of elements, limiting factors, organisms, fluxes, etc.

Most experimental studies focused on interactions, i.e. the interactions of the factors are considered (e.g. for 2-factorial ANOVA), for example eCO_2 and warming (reviewed by Dieleman et al., 2012), eCO_2

and N availability (reviewed by De Graaff et al., 2006; Reich et al., 2006; Sillen and Dieleman, 2012; Feng et al., 2015; Bowsher et al., 2018), eCO₂ and water availability (reviewed by De Graaff et al., 2014). Studies on the interactions of the *belowground processes* (not the factors) are extremely rare (Reich et al., 2006).

2.2. Examples of surprising and unexpected results based on interactions

A good example for such interspecies interactions and partly unexpected consequences for plant growth is C-N root-microbial competition (Fig. 2): 1) Plant production in total (Kudeyarov et al., 2006; reviewed by Norby and Zak, 2011; Jones et al., 2014), fine root production (Phillips et al., 2012; Drake et al., 2011) and rhizodeposition (Paterson et al., 1997) increase under eCO₂. Consequently, 2) more C will be added to soil. This leads to 3) higher availability of substrates for microorganisms, and thus to 4) microbial biomass increase with 5) higher N and P demand for microorganisms – increased microbial N and P immobilization. In turn, this leads to 6) less plant-available N and P in soil, triggering stronger competition between microorganisms and plants for N (Haase et al., 2007), resulting in N limitation for plants (Hu et al., 2001; Garten et al., 2011; Dieleman et al., 2012; Liang et al., 2016; Rütting, 2017; reviewed by Feng et al., 2015). The outcome of these cascading and backflow processes is that plant growth² and consequently C release into soil will be limited not by the atmospheric CO₂ concentration but by mineral N availability in soil. Despite the CO₂ fertilization, plant productivity may not increase because of decreasing plant-available N due to immobilization by microorganisms (Fig. 2). The limitation of plant growth will be switched from atmospheric CO₂ concentration to N (and P) limitation in soil (Garten et al., 2011).

Another interesting and surprising result of eCO₂ is related to the formation of soil aggregates (Rillig et al. 2001; Wilson et al., 2009). At first glance, there is no connection between CO₂ concentration in soil or atmosphere with aggregate formation and stability. Nonetheless, the higher C input into the soil and increased N and P limitations (Zak et al., 2000; Hu et al., 2001; Drake et al., 2011) stimulate mycorrhization of roots (Godbold and Berntson, 1997; Treseder, 2004; Alberton et al., 2005; Cheng et al., 2012). This stimulation and the benefits for plant grown under eCO₂ are especially strong for species associated with ectomycorrhizal fungi (Terrer et al., 2017). All mycorrhizal fungi release carbohydrates and proteins into the soil, and certain arbuscular mycorrhiza, e.g. *Glomus intraradices*, release glycoproteins such as glomalins in combination with extracellular polysaccharides produced by other rhizosphere microorganisms (Wilson et al., 2009). These compounds act as glue to bind soil particles, especially when soil dries, promoting the formation of larger and more stable aggregates. Accordingly, indirect effects of eCO₂ on mycorrhizal glucoproteins and other extracellular polysaccharides combine to boost soil aggregate formation and stability (Rillig and Mummey, 2006; Keidel et al., 2018 – only in 15–45 cm). This improves water and air permeability, increases water holding capacity and physically protects organic matter. Increasing soil moisture however (frequently measured in some FACE experiments, see below), may decrease aggregate size (Niklaus et al., 2003).

Given the promoted formation of large and stable aggregates (Rillig et al., 2001; Wilson et al., 2009) as well as additional C input by roots under eCO₂, the CO₂ concentration within aggregate pores (from a few

² Note that growth response of plants with C3 photosynthesis is higher than in C4 plants because the former type is much more dependent on atmospheric CO₂ concentration. The eCO₂ effects on C4 plants (increase by 12%) are far lower than on C3 plants (45% increase) (reviewed Poorter and Navas, 2003). Most conclusions drawn to date are relevant for C3 plants (all trees, shrubs, most crops, most herbs and grasses) but less so for C4 plants (maize, sorghum, *Miscanthus*, various prairie grasses), especially in the first decade of eCO₂ (Reich et al., 2018).

percent up to complete consumption and replacing oxygen, Nowak et al., 2015) increases more than under ambient CO₂. Consequently, chemo-autotrophic CO₂ re-fixation will rise (Beulig et al., 2016).

2.3. The well-known and most unknown effects of elevated CO₂ on belowground processes

Plant biomass production increases under eCO₂ (600–800 ppm) by about 13–20% (De Graaff et al., 2006; Ainsworth and Long, 2005; Feng et al., 2015) (but up to 200% for some crops; Rogers et al., 1994; Van Kessel et al., 2000a; Kudeyarov et al., 2006) compared to plants under ambient CO₂. Along with the direct effect of increased photosynthesis, certain indirect effects such as decreased abundance of plant-feeding nematodes and relative increase in bacteria- and fungus-feeding nematodes under eCO₂ contribute to increased plant growth (Mueller et al., 2016).

The indirect effects of eCO₂ on soil processes lead to an increase in root growth compared to aboveground biomass (Rogers et al., 1994; Arndal et al., 2018). Root biomass of grasses increases solely if eCO₂ is combined with N fertilization (meta-analysis of Sillen and Dieleman, 2012). The root biomass increase can be related to higher growth rates and/or root longevity. Both productivity and root morphology change under eCO₂: more fine and secondary roots have been recorded (Pregitzer et al., 1995; Treseder, 2004; Arndal et al., 2018). The association of roots with mycorrhizal fungi increases by 30% and 7% for ecto- (ECM) and arbuscular mycorrhizae (AMF), respectively (Treseder, 2004; Mohan et al., 2014; Terrer et al., 2016). Generally, eCO₂ effects on ECM are more positive and vary less compared to AMF (Mohan et al., 2014; Terrer et al., 2016). The eCO₂, however, does not affect overall ECM diversity, but alters the structure of ECM community due to faster development of few host-specific ectomycorrhizal groups (Parrent et al., 2006). Because both arbuscular (Cheng et al., 2012) and ECM (Lindahl and Tunlid, 2015) accelerates SOM decomposition to mine for N and P to compensate increasing shoot and biomass demand, we hypothesize that higher C input by plants will be compensated by faster SOM decomposition. SOM changes will therefore be marginal under eCO₂. Plants associated with ECM acquire N at a lower cost than plants associated with AMF (Terrer et al., 2018), and this ability is especially pronounced under eCO₂ and N limitation in soil. This causes changes in C allocation patterns, root morphology and especially of mycorrhizal to compensate for nutrients that become limiting (Luo et al., 2004; Lindahl and Tunlid, 2015).

An increase in fine and secondary roots often leads to an increase in rhizodeposition (including exudation, Phillips et al., 2011). This stimulates microbial activity (Paterson et al., 1997; Zak et al., 2000) and can accelerate microbial mobilization of nutrients in the rhizosphere (Cheng, 1999; Phillips et al., 2011). Increased fine roots as well as rhizodeposition stimulate CO₂ production (Phillips et al., 2012). This CO₂ is plant-derived – originating from rhizomicrobial respiration – and does not contribute to an increase of CO₂ in the atmosphere because this C is fixed initially by photosynthesis.

Besides morphological changes, the quality of litter and root residues will shift towards a higher C/N ratio and increase cellulose and lignin contents (Norby et al., 2001; Norby and Jackson, 2000; Cotrufo et al., 2005; Feng et al., 2015). Phenolics and tannins will also increase (McElrone et al., 2005). These shifts in plant tissue quality lower decomposition rates and prolong the residence time of litter and associated nutrients in soil (Cotrufo et al., 2005; Marhan et al., 2008).

The unknown effects of eCO₂ belowground are connected with processes indirectly driven by plants in soil. The unknown effects are on 1) microorganisms (including mycorrhiza): phylogenetic groups, activity, growth rates, turnover, functions, C and N cycling; 2) extracellular enzymes: functional types, kinetics and activities; 3) SOM: content, composition of pools, turnover, and localization within soil matrix; 4) weathering. These unknown effects will be analyzed in the next sections.

Table 2
Change of microbial biomass and microbial respiration under various plant groups grown under elevated CO₂ (extracted from Zak et al., 2000).

Plants	Microbial biomass	Microbial respiration
Graminoid	+ 17 ± 86	+ 34 ± 35
Herbaceous	+ 29 ± 29	+ 34 ± 19
Woody	+ 19 ± 46	+ 20 ± 23
Average	+ 22	+ 29

All data presented as % changes under elevated CO₂ versus ambient CO₂ (± SD).

2.4. Effects of elevated CO₂ concentration on microbial biomass and functions

Higher input of available C from roots into soil stimulates microbial growth and increases biomass (Table 2, Zak et al., 2000). Despite an average ~16% increase in microbial biomass C compared to soil under ambient CO₂, the variation (± SD) in biomass is very high: up to 86%. According to the recent review of 68 studies, the average microbial biomass C increase is 14% and N is 7.4% (Liu et al., 2018). Thus, the final effects depend on the specific soil conditions and are mainly controlled by N limitation (Runion et al., 1997; Sillen and Dieleman, 2012). The relative increase of CO₂ released by microbial respiration is higher than the increase in microbial biomass (Hagedorn et al., 2013), and the variation is much less than that of microbial biomass (Table 2). This indicates that fast production, allocation, and decomposition of the labile photosynthates do not affect microbial biomass (Drake et al., 2016). We therefore conclude that eCO₂ increases the flux (microbial respiration) more strongly than the pool (total microbial biomass) (McKinley et al., 2009; Hagedorn et al., 2013). Such a discrepancy helps predict the differences in the short- and long-term consequences of atmospheric CO₂ enrichment. Over the short-term (days to weeks), increased respiration reflects facilitation of C turnover in the rhizosphere rather than intensification of SOM decomposition (McKinley et al., 2009; Phillips et al., 2012; Van Groenigen et al., 2017). Over the long-term (months), however, such an increase in microbial activity might cause a priming effect (Hoosbeek et al., 2004; Cheng et al., 2014b; Drake et al., 2011), which would progressively affect both total soil C stock and microbial functioning (discussed in detail below, see section 2.8). Indeed, priming was more pronounced under eCO₂ versus ambient CO₂ (Trueman and Gonzalez-Meler, 2005), mainly affecting relatively old C pools (Vestergård et al., 2016). The abundance of functional genes related to the decomposition of organic compounds increased, but the abundance of genes responsible for the synthesis of specific labile compounds, e.g., glutamine, was reduced (Tu et al., 2017). Thus, eCO₂ accelerates microbial respiration and the CO₂ efflux from soil (Martens et al., 2009; Hagedorn et al., 2013), over the long-term depleting both particulate and stabilized SOM (Black et al., 2017).

Other important fluxes, reflecting microbial functions, also increased very strongly: total CO₂ efflux from soil (root and microbial respiration) increased by 45%, microbial N immobilization by 93% and net N mineralization by 44% compared to ambient CO₂ (reviewed by Zak et al., 2000). Based on a meta-analysis of 30 FACE and OTC studies, de Graaff et al. (2006) determined that soil CO₂ increased by 18%, whereas microbial biomass only by 7%. A similar, much stronger increase in soil respiration compared to microbial biomass under eCO₂ was reported based on more than 40 FACE studies (Dieleman et al., 2012). Despite the very high variation between individual studies, all show that most microbial processes will be accelerated under eCO₂.

Labile C (sugars, carboxylic acids, peptides, etc.) released by roots stimulates microbial growth. An increase in microbial growth rates revealed by substrate-induced growth respiration (SIGR) approach (Panikov, 1995) was consistent in three aggregate size fractions under summer wheat exposed to eCO₂ (Mini-FACE, Stuttgart-Hohenheim; Dorodnikov et al., 2009a). This increase (~10% per hour) means that,

after about 7 h of non-limited growth, the soil microbial biomass can double under eCO₂ compared to ambient CO₂. None of the FACE experiments, however, showed such a strong increase in microbial biomass because the SIGR approach reflects the potential growth rates – without limitations of easily decomposable substrate (i.e. glucose) and nutrients (N, P). Under limiting conditions (e.g. N, P deficiency), most extra-C released by roots is microbially processed without a strong increase in microbial biomass (Hagedorn et al., 2013). Consequently, the increase in the pools (i.e. microbial biomass) is much less than that of the activities (i.e. microbial growth rates), which are directly related to fluxes.

The eCO₂ presumably affects metabolically active rather than total microbial communities (Jossi et al., 2006). The accelerated specific microbial growth rates were confirmed for three FACE experiments on four plant species: there was a clear linear relationship between growth rates and CO₂ level (Blagodatskaya et al., 2010). Evidence that the eCO₂ effect was caused by altered rhizodeposits quality and quantity is supported by two-times higher increase in specific microbial growth rates in the rhizosphere compared to soil more distant from the roots (Blagodatskaya et al., 2010). Remarkably, the microbial response to eCO₂ was much stronger when growth was induced by simple (glucose) vs. complex (yeast extract) substrates. This indicates activation of microorganisms with lower auxotrophic requirements under eCO₂ (Freeman et al., 2004; Da Costa et al., 2018). The expected increase in plant assimilated C (up to 32%) under eCO₂ is accompanied by a much smaller increase in plant N uptake (up to 20%) (Luo et al., 2006). This results in a broader C:N ratio in both shoots and roots (Cotrufo et al., 2005; Luo et al., 2006; Lichter et al., 2008; Feng et al., 2015). Remarkably, the response of the C:N ratio to eCO₂ was much lower in litter and SOM versus living plants. This indicates stronger C versus N losses during decomposition of plant residues (meta-analysis: Luo et al., 2006) and more intensive N recycling in the ecosystem.

An increased rhizodeposition with a higher C/N ratio under eCO₂ versus ambient CO₂ decreases microbial species diversity (Lesaulnier et al., 2008; Da Costa et al., 2018). It also selects for microorganisms with lower auxotrophic requirements, i.e. those capable of rapid growth on energy-rich, simple substrates (Freeman et al., 2004) leading e.g. to lower C use efficiency (Van Groenigen et al., 2015). Thus, larger C input from plants is compensated by its faster decomposition in soil due to accelerated microbial growth and enzyme activities (see below).

The increase in microbial-specific growth rates due to eCO₂ was much stronger under N limitation, whereas N addition flattened the effect (Blagodatskaya et al., 2010). Thus, the effect of eCO₂ (faster microbial growth) can be counterbalanced by N fertilization. This calls for the studies on dual (direct and indirect) N effects on plant-microbial interactions in the rhizosphere under eCO₂ (Dieleman et al., 2012). Nitrogen addition directly increases microbial C use efficiency (Blagodatskaya et al., 2014) and indirectly increases fine root production (Phillips et al., 2012). Thus, eCO₂ boosts plant-microbial competition for N over both the short- (days) and medium-term (weeks - months) (Fig. 2). A consequence of these direct and indirect N effects is the long-term domination of more efficient but slow-growing microorganisms able to mine for N from SOM by producing extracellular enzymes (Fontaine et al., 2003).

2.5. Effects of elevated CO₂ on N cycling processes

The increase in atmospheric CO₂ concentration did not change the N content in plants if mineral N is sufficient in soil, and has no strong effect on the soil N over the short term (Pastore et al., 2016). It also had no effects on either autotrophic nitrifiers (Hu et al., 2016) or nitrate-reducing microorganisms (Marhan et al., 2011). Over the long term, however, N cycling pathways were selectively affected. For example, eCO₂ stimulated specific microbial functions such as N₂ fixation (van Groenigen et al., 2006; Trierweiler et al., 2018) and the dissimilatory nitrate reduction by increasing the abundance of the corresponding

genes (Haase et al., 2007). A strong increase in N₂ fixation by legumes can be increasingly limited by P and molybdenum (Trierweiler et al., 2018). In contrast, the genetic potential for anaerobic ammonium oxidation was strongly reduced under eCO₂ (Tu et al., 2017).

As noted above, the effects of eCO₂ on plants depends on N availability. Under N limitation, eCO₂ retarded SOM decomposition (Hungate et al., 2009). In N-rich ecosystems, however, eCO₂ increased enzyme activities in the rhizosphere (Meier et al., 2014) e.g. chitinase (Dorodnikov et al., 2009b) and stimulated the activity and growth of denitrifiers, which outcompeted plants in nitrate uptake (Wu et al., 2017). Individual studies showed a strong increase in N₂O emissions because of higher soil moisture stimulating denitrification and nitrification from SOM mineralization under eCO₂ (Moser et al., 2018). The increase in N₂O emissions was marginal (4.6%) averaged over 88 studies (Liu et al., 2018). Despite the potential for greater N losses over the short term (e.g. by increased mineralization, Reich et al., 2018), eCO₂ increased N accumulation at the ecosystem level over the long term (Pastore et al., 2016). This involved higher N₂ fixation in the first few years (Hungate et al., 2004) and more complete N recycling later (Phillips et al., 2012).

Deeper root growth especially in forests was frequently observed in the FACE experiments (Iversen et al., 2011; McKinley et al., 2009). Two potential reasons may promote deeper root growth: i) water limitation in the topsoil, or/and ii) nutrient limitation. The water limitation hypothesis should be rejected because lower stomatal conductance at eCO₂ (Warren et al., 2011) leads to about 10% less water losses and thus to higher soil moisture (Leuzinger and Körner, 2007). Nitrogen limitation in topsoil, however, induced by eCO₂ causes roots to explore for new N resources in soil. Faster N mineralization from SOM (McKinley et al., 2009), paralleled by slightly higher soil moisture, leads to deeper N allocation in soil (down to the groundwater) and thus to deeper root growth. Accordingly, the N limitation for plants will be compensated not only by accelerated N (re)cycling in the topsoil, but also by roots exploring deeper resources. This means that larger soil volumes will be involved in C and N cycling under eCO₂. We assume that this is valid not only for N and other nutrients stored in SOM (P, S) but also for nutrients and nonessential elements mobilized by accelerated weathering of the saprolite (see below).

2.6. Effects of elevated CO₂ on extracellular enzymes

Soil enzyme activities reflect the specific microbial functions in the decomposition of polymeric organic substances and in nutrient mobilization (Burns et al., 2013). Most studies on soil enzymes under eCO₂ were done for hydrolytic enzymes contributing to C, N and P cycles (more seldom for S). As compared to ambient CO₂, the 5 years under eCO₂ doubled the response of hydrolytic enzymes to added glucose (as an analogue of root exudates) in soil under wheat (Dorodnikov et al., 2009b). This confirmed accelerated C turnover in the rhizosphere under eCO₂ (Phillips et al., 2011, 2012; Drake et al., 2011). eCO₂ mainly stimulated enzymes related to the N cycle and to microbial turnover (i.e. N-acetyl-glucosaminidase) indirectly (Dorodnikov et al., 2009b). This effect was most pronounced in medium-sized macroaggregates (0.25–2 mm) (Fig. 3) – the preferential location of growing roots. The 2-year FACE study in semiarid grassland showed a 3–10% increase of 14 genes responsible for C cycling enzymes and 0–20% increase of genes for N cycling enzymes – most of them closely correlated to soil moisture increase (Yu et al., 2018). Increased activities of oxidative enzymes (peroxidases and oxidases) (Finzi et al., 2006) points to an increasing role of fungi (main decomposers of lignin and cellulose, Kirk and Farrel, 1987) in litter decomposition under eCO₂. This reflects the increased lignin and cellulose content under eCO₂ (Cotrufo et al., 1994; Phillips et al., 2012), which increase extracellular enzymes: eCO₂ increases lignin content in litter; fungi produce more extracellular enzymes for their decomposition and N acquisition (Finzi et al., 2006). This is also supported by an increased fungal dominance relative to bacteria under

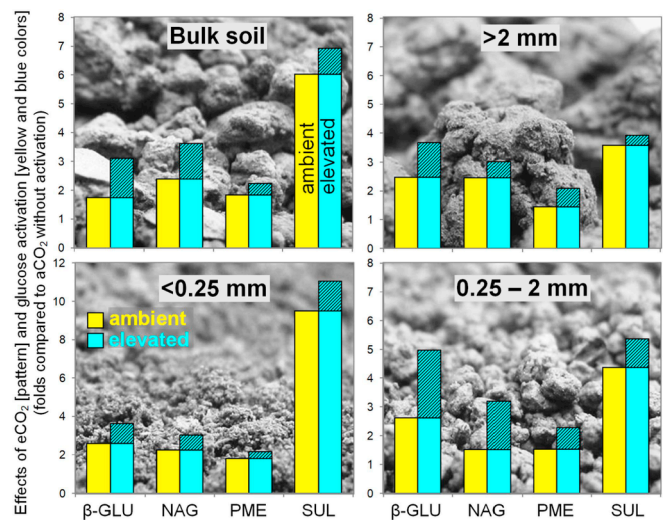


Fig. 3. Effects of 5-years elevated CO₂ on activities of β -glucosidase (β -GLU), N-acetyl-glucosaminidase (NAG), phosphomonoesterase (PME), and sulfatase (SUL) in bulk soil under summer wheat and three aggregate-size classes (> 2 mm, 0.25–2 mm, and < 0.25 mm) after activation with mixture of easily available C source (glucose) and mineral salts as nutrients (N, P, K, S, Mg elements). The effects of elevated CO₂ as well as glucose + nutrients activation on enzyme activities (shaded bars) were significant in comparison to respective controls ($p < 0.05$) (Mini-FACE Stuttgart-Hohenheim, Dorodnikov et al., 2009; modified).

eCO₂ (Dam et al., 2017). This, in turn increased the abundance of fungivorous nematodes, thus, demonstrating enhanced interactions within soil food webs induced by eCO₂.

The enzymatic response to eCO₂ varied strongly within heterogeneous soil microhabitats, along and across roots, since both roots and microorganisms produce exoenzymes. The eCO₂ induced functional niche differentiation between the rhizosphere and hyphosphere, as well as between root tips, mycorrhizal hyphae and along the root. This was revealed by 6-fold increase in the activity of N-releasing enzymes in the rhizosphere than in the hyphosphere under eCO₂ versus ambient CO₂. In contrast, the activity of C-degrading enzymes increased 6-fold in the hyphosphere versus rhizosphere (Meier et al., 2014). This suggests a stimulating effect of roots on N-cycling (not on N pools), whereas mycorrhizal fungi may contribute more to SOM decomposition under eCO₂ (Cheng et al., 2012).

2.7. Effects of elevated CO₂ on soil organic matter turnover and dissolved organic matter

Soil organic matter is one of the most stable C pools in terrestrial ecosystems. Its change in size and turnover is therefore usually small compared to most other C pools. Most FACE experiments (with maximum duration up to 2 decades) have shown no (van Kessel et al., 2000b; Keidel et al., 2018) or only marginal SOM changes (Lichter et al., 2008), especially without nutrient addition (reviewed by de Graaf et al., 2006; Luo et al., 2006; Hungate et al., 2009; Norby and Zak, 2011; Liu et al., 2018). The contents of SOM pools allocated between or inside different-sized aggregates as well as associated with soil minerals remained nearly stable (Dorodnikov et al., 2011). Even though most of the roots and thus root litter are located between aggregates or within macroaggregates, C stabilization is ongoing in microaggregates (Jastrow et al., 2005; Gunina and Kuzyakov, 2014) and in the clay fraction (Martens et al., 2009). This facilitates the formation of long-lived organo-mineral complexes.

The responses of NPP and SOM stock to eCO₂ are strongly misbalanced. Thus, an annual increase in plant productivity by 13–20% yr⁻¹ under elevated, corresponded to total SOM increases of only by

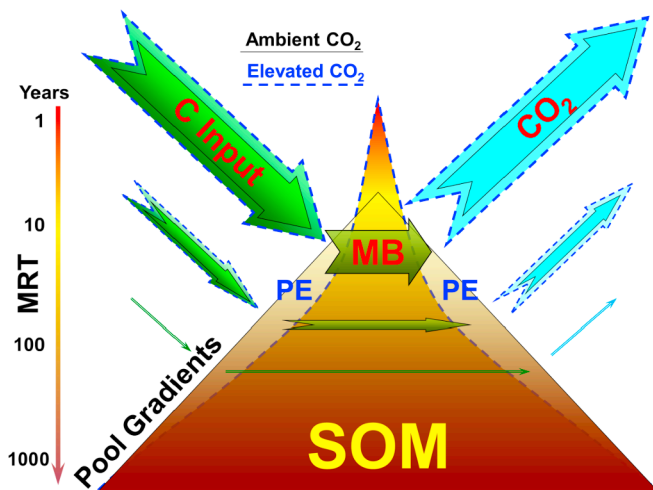


Fig. 4. Effects of elevated CO_2 on C pools and fluxes in soil: The size of the SOM pool (triangle) remains nearly the same, but fluxes (arrows) will be strongly accelerated. Arrows: fluxes into (green), through and from (blue) soil. Triangle: soil organic matter (SOM) presented as gradient of pools with very large old C stock (log MRT) and very small C pools with fast turnover. Blue dashed lines: changes in C fluxes and SOM properties under elevated CO_2 compared to ambient CO_2 (continuous lines). MRT: mean residence time. PE: priming effect. MB: microbial biomass. Despite a strong increase of input and output fluxes (here ~ 1.7 times) under elevated CO_2 , the SOM stock remains nearly the same. It is especially difficult to measure the changes in SOM stocks because the decrease of some pools with intermediate MRT is nearly compensated by the increase of pools with very fast MRT. Arrow sizes reflect flux intensities into SOM, within SOM and out of SOM. The MRT is inverse to flux size.

1.2–2.2% of the C stock (based on a review of 59 studies: De Graaff et al., 2006; based on 89 studies: Liu et al., 2018). One of the biotic mechanisms of marginal to none SOM accumulation despite higher C input is a strong increase in ectomycorrhiza under eCO_2 (Terrer et al., 2016), which co-metabolically accelerates SOM decomposition to mine for N (Lindahl and Tunlid, 2015) and P (Jin et al., 2015). As a result of N and P mining, C will be lost as CO_2 from soil. If N is sufficient for plant and microbial growth, or N is added by fertilization, SOM decomposition decreases, and more C can be sequestered in soil under eCO_2 compared to ambient CO_2 (De Graaf et al., 2006; Reich et al., 2006; Hungate et al., 2009; Norby and Zak, 2011). Nonetheless, this effect is much smaller than the increase of C input to soil, and is not a relevant option for mitigating a CO_2 increase in the atmosphere. We therefore conclude again that soil C pools remain comparatively stable under eCO_2 , and that effects on stable pools such as SOM are hardly measurable (Luo et al., 2006; Norby and Zak, 2011).

Although SOM stocks do not change, this steady state involves a continuous replenishing: new formation and decomposition. This could be altered under eCO_2 (Fig. 4). To detect changes in SOM, the isotopic tracing approach using natural $\delta^{13}\text{C}$ shift of CO_2 has been widely applied (van Kessel et al., 2000a, 2000b) (Table 1). The isotopic composition of CO_2 used in eCO_2 studies (e.g. in FACE studies) is usually derived from fossil fuel, which is depleted in ^{13}C ($\delta^{13}\text{C}$ varies from -35‰ to -50‰) compared with atmospheric CO_2 ($\delta^{13}\text{C} - 8\text{‰}$) (Hungate et al., 1996; Van Kessel et al., 2000a). Plants grown in a ^{13}C -depleted eCO_2 atmosphere produce litter and rhizodeposits which, upon incorporation into SOM, decrease its $\delta^{13}\text{C}$. The contribution of the new FACE-derived C to total SOM and its turnover can be calculated based on the $\delta^{13}\text{C}$ of the SOM under ambient conditions in contrast eCO_2 conditions (van Kessel et al., 2006). More than 2/3 of the CO_2 efflux from soil in the Duke-FACE came from C pools with a turnover time of about one month, and the remaining 1/3 came from pools with decadal C turnover times (Taneva et al., 2006). Across many FACE studies, the mean residence time (MRT) of C in SOM varied from 3 to 4

years (van Kessel et al., 2006; Lichter et al., 2008) to 40–50 (Dorodnikov et al., 2011) and more than 100 years (Crow et al., 2009). Accelerated SOM turnover under eCO_2 appears to be an established phenomenon (Thaysen et al., 2017; van Groenigen et al., 2015, 2017) involving higher C input and faster decomposition (Fig. 4). Accordingly, we expect an accelerated turnover of young and old SOM pools (van Groenigen et al., 2015) and a faster inclusion of relatively inert SOM pools in the C cycle (Heath et al., 2005).

Dissolved organic matter (DOM) is an important constituent of SOM because its availability for microorganisms and transport with associated nutrients (N, P) to subsoil (Bol et al., 2016). Changes in DOM could help predict SOM transformations based on its high mobility and relative availability to decomposition. This is because DOC is more sensitive to changing environmental conditions than SOM (Guillaume et al., 2016). The above-mentioned intensified SOM decomposition under eCO_2 is further confirmed by increasing DOM pools observed in various ecosystems. For example, for forests, the annual increase of DOM inputs into soil was 50% (Phillips et al., 2011; Hagedorn et al., 2008); for modeled grassland communities, the DOM pool increased up to 70–110% above the ambient CO_2 treatment (Jones et al., 1998). On a global average, the DOC increase was ~ 1.5 times larger than changes in the SOM under eCO_2 (review of 36 studies, Liu et al., 2018). These results imply that eCO_2 will have a major impact on easily available C pools (Van Groenigen et al., 2017) such as DOM (Fig. 4). Although part of the DOM is released from increased litter inputs (Hagedorn and Machwitz, 2007), most of it is produced from SOM. The increasing DOM production under eCO_2 clearly shows accelerated C cycling and priming of SOM (Hagedorn et al., 2008). Nonetheless, because the DOM pool is very small compared to total SOM, the eCO_2 effect on DOM changes cannot strongly affect total SOM.

2.8. Priming effects under elevated CO_2

Increased rhizodeposition and litter input under eCO_2 requires may increase priming effects, i.e. accelerated SOM decomposition caused by an increase in labile C input (Paterson et al., 1997; Cheng and Johnson, 1998; Cheng et al., 2014b; Drake et al., 2011). This is especially important considering the interactive effects of eCO_2 : higher plant C input belowground, intensive microbial N immobilization (see above) (van Kessel et al., 2000b; Reich et al., 2006) and N (re)cycling in microorganisms (Phillips et al., 2011, 2012). Nitrogen fertilization decelerates microbial growth (Blagodatskaya et al., 2010) and increases their growth efficiency (production of new biomass per added C). This favors K strategists able to produce enzymes for decomposing recalcitrant SOM (Schimel and Shaffer, 2012). Therefore, stronger priming and decomposition of old SOM pools are expected under eCO_2 (van Kessel et al., 2000b; Paterson et al., 2008; Langley et al., 2009) (Fig. 4). This was suggested as one of the main reasons for the absence of C accumulation under eCO_2 in soil (Langley et al., 2009; Billings et al., 2010; Hagedorn et al., 2008; Hoosbeek et al., 2004). However, interaction of two contrasting effects, namely, facilitation of microbial growth by eCO_2 and growth retardation by N fertilization, still results in accelerated specific growth rates up to 5–23% under eCO_2 versus ambient CO_2 . Therefore, higher C input under eCO_2 will be compensated by faster microbial turnover and may also be responsible for the apparent priming and the absence of SOM increase (Phillips et al., 2012). Absence of SOM increase despite higher C input through litter and rhizodeposition point to accelerated SOM turnover under eCO_2 (Langley et al., 2009). That acceleration decouples C and N (and probably other nutrient) cycles because mineralized C will be released from soil as CO_2 , but mineral N remains and will be (re)used by microorganisms (Phillips et al., 2012) and plants to cover their increased N demand.

In natural ecosystems, one possible consequence of eCO_2 is a shift in plant communities due to invasion of plants with a strong ability for N acquisition, e.g. invasive species (Dukes and Mooney, 1999; Smith et al., 2000; Wolkovich et al., 2010). Fast N uptake by roots of strong

competitors forces microorganisms to mineralize more N from SOM, i.e. priming. This will be more pronounced under N limitation. In contrast, native plant communities mitigate N limitation in the rhizosphere by intensively releasing available C that stimulates faster turnover in microorganisms and N release from microbial biomass (Blagodatskaya et al., 2014; Phillips et al., 2012) and from SOM (Phillips et al., 2011; Langley et al., 2009).

2.9. Effects of elevated CO₂ on water budget and soil temperature

The evolutionary tradeoff of plants is to increase the CO₂ uptake from the atmosphere and to decrease water losses through the stomata. The water losses from soil per unit of plant biomass under eCO₂ decreases (Norby and Zak, 2011) resulting in increased water use efficiency (WUE). The less water consumption per unit of produced biomass is partly compensated for by higher plant biomass production per area. Therefore, the consequences of higher WUE on soil moisture depend on specific soil-plant combinations and climate conditions. Some studies reported on average ~3% increase in soil water content in a temperate grassland (Andresen et al., 2018) while another study observed > 10% (Moser et al., 2018; Leuzinger and Körner, 2007; Manderscheid et al., 2014), some only observed only marginal or no changes e.g. by Duke-FACE (Drake et al., 2016). Therefore, it is hard to generalize the future soil water relations across various ecosystems. Geological records clearly show that the drop in stomatal conductance at the Triassic–Jurassic boundary transition resulted from rising CO₂ lead to higher soil water content and simultaneous increases in runoff and erosion rates (Steinthorsdottir et al., 2012). Modeling studies simulating up to 1120 ppmv CO₂ clearly show a strong increase (up to 20%) of drainage because of decreasing evapotranspiration (Beaulieu et al., 2010). If soil moisture does increase under eCO₂, it will have various consequences at the ecosystem level: 1) Groundwater will increase in humid climates (Beaulieu et al., 2010) and in those areas where hydrothermal coefficient is > 0.8. Especially in areas where evapotranspiration outbalances precipitation, the estimated 10% higher soil moisture (Leuzinger and Körner, 2007; van Ittersum et al., 2003) may double groundwater formation. Consequently, 2) leaching cations (mainly Ca²⁺, Mg²⁺) and anions (NO₃⁻, SO₄²⁻) will decrease nutrient availability in the topsoil (McKinley et al., 2009; Siemens et al., 2012). 3) The shift in nutrient availability to the subsoil and groundwater could lead to deeper root growth (Iversen et al., 2011; McKinley et al., 2009) and deeper rhizodeposition with consequences for shifting microbial communities and activity, C and N mineralization cycling, and weathering (see below). 4) Increasing soil moisture may potentially trigger stronger water erosion/runoff (Leuzinger and Körner, 2010; L. Cheng et al., 2014). Although the runoff increase under eCO₂ seems to be very small in forested areas (< 3%, Leuzinger and Körner, 2010), it may have stronger consequences in open landscapes by creating water-saturated soils and especially through interactions with an increasing frequency and intensity of extreme precipitation events. 5) Water stress under drought conditions will drop – both for plants and microorganisms leading to higher plant C input into soil, but also faster SOM decomposition (Marhan et al., 2010). 6) Higher soil moisture could decrease wind erosion. 7) Lower water transpiration by plants increases canopy temperature by 1.5 °C (Long et al., 2006) to 2 °C (Burkart et al., 2011). This strong increase, however, may not necessarily increase soil temperature.

The eCO₂-induced changes in ‘small’ stomata far aboveground will lead to a broad range of outcomes depending on the soil water content. In forest FACE studies on fertile soils in temperate climates (e.g. the Duke Forest FACE), the decreased stomatal conductance was compensated by a higher leaf area index (Ainsworth and Long, 2005; Hungate et al., 2006). This means other changes (higher groundwater levels, larger leaf area) may be compensated for by decreased plant water consumption. In semiarid climates, however, even a slight increase in soil moisture may be especially relevant and will lead to less drought

stress for microorganisms and plants. Generally, nearly all indirect effects of eCO₂ on soil processes are stronger in (semi)arid ecosystems (Fatichi et al., 2016), because decreased transpiration increases soil moisture relieving water limitation.

2.10. Incorporation of C from elevated CO₂ into soil carbonates

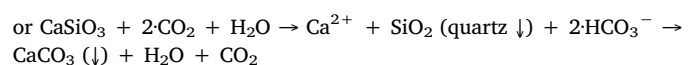
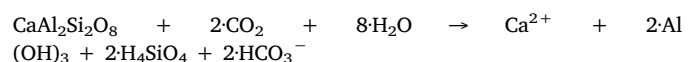
Nearly all studies from 151 FACE experiments globally (Jones et al., 2014) focused on organic soil C pools. No papers present the effects of eCO₂ specifically on inorganic C in soil – on pedogenic, biogenic or geogenic carbonates – mainly in the form of CaCO₃. Compared to 1500 Pg organic C in the upper 1 m (IPCC, 2014), soils contain 700–750 Pg inorganic C in 1 m depth (Batjes, 1996) – mainly in semiarid and arid areas (7.49·10⁹ ha; ca. 54% of the global land surface). These stocks of carbonates are large and could rival organic C pools. Their relevance increases compared to organic C since they have a millennial mean residence time (Schlesinger, 1985; Zamanian et al., 2016) however, their small formation rate makes this pool irrelevant on the scale of decades or centuries. Furthermore, when a soil is under steady state, the root- or microbially derived CO₂ (originating from the atmosphere) is in exchange with CaCO₃ without effecting soil C stocks.

Recent findings show carbonates can be involved in short-term biological C cycles at a much faster rate than expected based on: 1) The MRT of C in pedogenic CaCO₃ is probably much shorter than estimated initially for the Mojave Desert (~78,000 years, Schlesinger, 1985) and ranges within a few thousand years (Kuzyakov et al., 2006; Gocke et al., 2011). 2) Leaching of cations because of slightly higher soil moisture (see above) and a (much) higher cation concentration in the soil solution (Karberg et al., 2005) under eCO₂ leads to Ca²⁺ and Mg²⁺ removal (Siemens et al., 2012; Williams et al., 2003) that influences the CaCO₃ equilibrium release of CO₂ to the atmosphere (Schlesinger, 2017). 3) A strong increase in rhizodeposition (see above), including the release of organic acids under eCO₂, will acidify the soil and release CO₂ from CaCO₃. 4) Higher N fertilization and N₂ fixation by legumes will accelerate soil acidification globally (Zamanian et al., 2018). This will likely shift the CaCO₃ equilibrium to CO₂ release into the atmosphere (Zamanian and Kuzyakov, 2019).

The complexity of these and other processes was rarely or never considered in FACE studies, and only three papers mention the increased carbonate concentration in soil solution (Williams et al., 2003; Karberg et al., 2005; Siemens et al., 2012). Without acidification and/or Ca²⁺ leaching from soil, eCO₂ will not affect the carbonate stocks. Nonetheless, we speculate that the exchange between carbonates and CO₂ in soil will be strongly accelerated. This means an increased vulnerability of CaCO₃-containing soils to loose CO₂ to the atmosphere. The processes transferring large stocks of carbonates into biotic C cycles should thus be considered because such effects, though driven by natural processes, are well known in Earth history, e.g. between the Pleistocene and Holocene, when around 400–500 Pg C was released from carbonates and strongly intensified global warming over a short period (Adams and Post, 1999).

2.11. Effects of elevated CO₂ on biochemical weathering and nutrient release

Over geological time scales, the atmospheric CO₂ concentration is consumed by rock weathering (mainly Ca- and Mg-containing silicates):



This direct abiotic removal of CO₂ from the atmosphere will be accelerated 2.4%–5% (depending on the rock composition) per 100 ppmv increase in CO₂ (Beaulieu et al., 2010) and can lower the

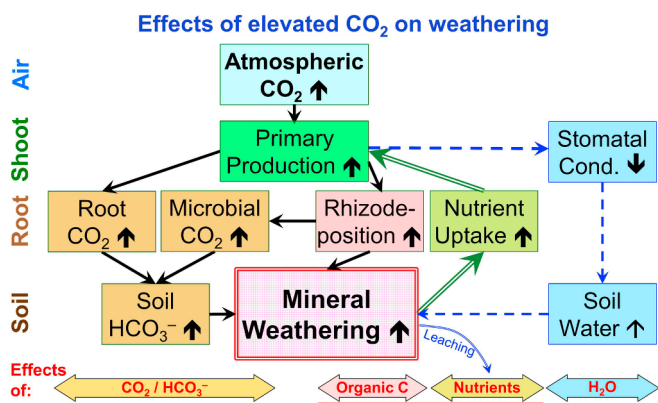


Fig. 5. Conceptual diagram of relationships between elevated atmospheric CO₂ (Atmospheric CO₂ ↑) and the rate and extent of mineral weathering in soil. Black arrows between boxes: direction of C fluxes from plant to soil pools; green and blue double arrows: uptake of nutrients from soil solution by plants and leaching, respectively; blue dashed arrows: slightly increasing water content in soil because of decreased stomatal conductance. Short bold arrows within boxes: increase (↑) or decrease (↓) of individual processes. The weathering under elevated CO₂ increases because of: 1) More weathering agents: 1a) HCO₃⁻, 1b) organic acids, 1c) chelating agents, and 1d) water; 2) Stronger plant uptake of ions (nutrients and nonessential elements) released from weathered minerals; 3) Higher soil water content increasing solubilization of elements; and 4) Stronger leaching. The strongest effects are connected with the release of organic acids and with nutrient uptake by plants (underlined). All processes and fluxes in soil increase (↑) under elevated CO₂.

increasing CO₂ concentration by 30–300 ppm over the next 100 years (Taylor et al., 2016).

The indirect effects of eCO₂ on weathering and belowground mobilization of elements: nutrients (K, Ca, Mg, S, Fe, micronutrients) and nonessential elements (Na, Si, Al, Cl, Fe excess) are more important than the direct impacts (Brantley et al., 2011). Plants accelerate silicate weathering by at least 2–8 folds relative to abiotic processes (reviewed by Song et al., 2012). eCO₂ accelerates mineral weathering through vegetation and microbial pathways (Fig. 5). As presented above, the increased primary productivity of plants accelerates respiration of both autotrophs (roots) and heterotrophs (most microorganisms in soil). This increases soil CO₂ concentration which then increases production of carbonic acid (HCO₃⁻), a major weathering agent (Andrews and Schlesinger, 2001; Oh et al., 2007; Song et al., 2012; Beaulieu et al., 2010). Considering the improved water use efficiency by plants under eCO₂ (via decreased stomatal conductance, e.g. Körner, 2000) and the slightly increasing water content in soil, the formation of carbonic acid could be additionally promoted (Song et al., 2012). Note, however, that the relative increase in soil CO₂ concentration is much smaller compared to the increase of plant growth (Andrews and Schlesinger, 2001). Therefore, the additional release of H⁺ and organic acids by roots contributes to mineral weathering by order(s) of magnitude stronger than an increase in respired CO₂.

Along with the CO₂-derived carbonic acid, the increased root exudation (Paterson et al., 1997; Phillips et al., 2011) containing acids (mainly carboxylic acids, and other chelating agents) further promotes weathering of primary and secondary minerals in soils and parent materials (Fig. 5). For example, only 2 years of eCO₂ under loblolly pine resulted in a 271% increase in the cation concentration of soil solution, a 162% increase in alkalinity, and a 25% increase in Si (Andrews and Schlesinger, 2001). Still, the strong boost in (bio)chemical weathering under eCO₂ (Karberg et al., 2005; Song et al., 2012) is counterbalanced by reported insignificant differences in chemical weathering rates versus ambient atmospheric CO₂ (Oh et al., 2007). For CO₂ concentrations similar to that in the atmosphere, weathering increases as the power function ($Dissolution = P_{CO_2}^{0.45}$; Navarre-Sitchler and Thyne, 2007). This relationship may reflect the poor chemical weathering at

ambient CO₂ concentrations in the atmosphere. However, this is irrelevant in terms of biochemical weathering (in the environment of organic acids, other chelating agents and high H⁺ concentration) and also in soil and regoliths, where CO₂ concentrations are 1–3 orders of magnitude higher than in the atmosphere. Therefore, no conclusive evidence is available to predict changes in elemental fluxes from the mineral phase, at least not over the short term (Williams et al., 2003). The absence of clear statistical significance of eCO₂ on weathering mainly reflects the very high variation of soil solution chemistry and confounding N effects (Williams et al., 2003). Mesocosm studies under controlled conditions, and especially long-term field-based eCO₂ experiments, are needed to predict decadal and centennial changes in chemical denudation fluxes across ecosystems (Banwart et al., 2009).

Other consequences of increased soil moisture under eCO₂ in topsoil and subsoil are: 1) shifts in the solid-liquid phase equilibrium to the liquid phase, 2) increases in element stocks in soil solution and thus, both of which can accelerate weathering (Fig. 5). Furthermore, weathering will be accelerated because of increased biological pumping – plant removal of nutrients and nonessential elements under eCO₂ (Song et al., 2012) as well as higher leaching losses (Steinhorsdottir et al., 2012), which may be expected after flash rains remove higher cation contents under eCO₂. Further, if erosion will increase because of higher soil water content (Steinhorsdottir et al., 2012), the weathering saprolite zone will move closer to the surface, and additionally accelerate the release of nutrients from rocks (Brantley et al., 2011). Despite accelerated weathering, the nutrient stock in the soil will not strongly increase because of continuous removal by harvest (for agricultural crops) and leaching (for most forests). This confirms the hypothesis that the fluxes will increase more strongly than the pools.

3. Conclusions

Elevated CO₂ in the atmosphere affects various parts of ecosystems including soils. It affects soil processes indirectly: by the interaction between higher C input by plants, increased microbial biomass and activities, stronger N limitations (and probably other nutrients), and by changes in water regimes (Fig. 5). Most of these indirect effects are related to the shift in factors limiting plant and microbial growth and to the interactions between available C and N in soil. These indirect effects are larger in water-limited ecosystems (Fatichi et al., 2016). In summary, eCO₂ accelerates the following processes and fluxes: C input into soil, microbial N immobilization, mineralization and turnover of SOM, microbial biomass turnover, microbial activities including growth rates and respiration, enzyme activities, priming effects, aggregation (size and stability), CaCO₃ dissolution and CO₂ release into the atmosphere, soil moisture and nutrient leaching, as well as weathering of primary and secondary minerals. Finally, eCO₂ will decrease the decomposition rates of plant residues above- and belowground and will reduce N availability in soil.

Based on the broad range of plant and soil processes affected by eCO₂, we conclude that its effects are much larger on fluxes than on pools (Fig. 4). This is clearly demonstrated by comparing changes in C input to soil with total C content, comparing SOM stocks with CO₂ fluxes from soil, microbial biomass with microbial activities, DOM content with production, carbonate stocks and their exchange with CO₂, and weathering and release of cations. In most cases the pools remained nearly the same under eCO₂ compared to ambient CO₂ levels, but the fluxes strongly increase. Note here that with few exceptions (Hagedorn et al., 2013; Van Groenigen et al., 2017; Xue et al., 2017), most studies are based on measurements of pools rather than fluxes. Measuring pools frequently fails to capture the real changes under eCO₂ as well as under certain other Global Change effects.

In conclusion, we state that the eCO₂ concentration in the atmosphere has no (or very minor) effects on the pools, but strongly increases the fluxes (Fig. 4). Consequently, eCO₂ will accelerate biogeochemical cycles.

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