Impacts of atmospheric CO_2-enrichment on the functional diversity of collembolans and nematodes in an agroecosystem

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Poster

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Vorwort

Im Rahmen der vorliegenden Dissertation wurde der Einfluss des atmosphärischen CO_2-Anstiegs auf die funktionelle Diversität der Collembolen- und Nematodengemeinschaft eines Agrarökosystems unter Anbau von Zuckerrüben und Winterweizen zu jeweils zwei Pflanzenentwicklungsstadien untersucht. Die stabile C-Isotopenanalyse der verschiedenen Collembolenarten und Ernährungstypen der Nematoden lieferte Einblicke in veränderte Interaktionen und den C-Transport innerhalb des Bodennahrungsnetzes unter zukünftigen Bedingungen. Da die Auswirkungen des atmosphärischen CO_2-Anstiegs auf Agrarökosysteme von maßgeblicher Wichtigkeit für die zukünftige, nachhaltige Ernährungssicherung, und bisher wenig verstanden sind, liefert die vorliegende Arbeit im Kontext des Klimawandels und Biodiversitätsschutzes einen wichtigen Beitrag zur Verbesserung des Kenntnisstandes hinsichtlich von Bodenprozessen.

Die Dissertation gliedert sich in drei Teile. Der erste Teil umfasst die Einleitung, unterteilt in 6 Unterkapitel, in der der Hintergrund der durchgeführten Untersuchungen dargelegt und erläutert wird, sowie eine kurze Darstellung der Ziele der Dissertation.

Den zweiten Teil der Arbeit stellen drei rezensierte Publikationen dar, in denen Teile der durchgeführten Untersuchungen in international renommierten Fachzeitschriften veröffentlicht wurden. Der erste Artikel (2.1) behandelt eine Methodenstudie hinsichtlich der Anwendbarkeit von Aufbereitungs-, Konservierungs- und Fixierungsverfahren für Collembolen und Nematoden im Rahmen der stabilen C-Isotopenanalyse. Der zweite Artikel (2.2) umfasst die Beeinflussung der Collembolenarten und –lebensformtypen, der dritte (2.3) die der Ernährungstypen der Nematoden durch den atmosphärischen CO_2-Anstieg.

Eine integrierende Diskussion der gesamten Ergebnisse sowie Schlussfolgerungen und Ausblicke bilden den dritten Teil der Arbeit.

Anteil der Autoren an der Arbeit und den Artikeln

An der Veröffentlichung der Ergebnisse der Arbeit waren Herr Prof. Dr. Hans-Joachim Weigel als Initiator und Hauptverantwortlicher des FACE-Versuchs und Leiter des Institutes für Biodiversität des Johann Heinrich von Thünen Institutes (vTI); Frau Dr. Anette Giesemann als Leiterin der Arbeitsgruppe für stabile Isotopenanalysen am Institut für Agrarrelevante Klimaforschung des vTI; sowie Prof. Dr. Stefan Schrader als Leiter der Arbeitsgruppe „Funktionelle Bodenzoologie“ des Institutes für Biodiversität des vTI, und Mentor der vorliegenden Dissertation, als Co-Autoren beteiligt. Die Entwicklung des Konzepts, dass im Rahmen der Dissertation verfolgt wurde, alle Ideen und Arbeiten, die Auswertung der Ergebnisse, sowie das Ausarbeiten und Verfassen der Artikel wurden von Frau Dipl. Biol. Christine Sticht durchgeführt.

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Summary

Within the present thesis, impacts of atmospheric CO_2-enrichment on the collembolan and nematode community of an agroecosystem, cultivated in a crop rotation, were analysed. The study was part of a long-term CO_2-enrichment field experiment (FACE: Free Air Carbon Dioxide Enrichment), which was performed at the Johann Heinrich von Thünen Institute (vTI) in Braunschweig. Samples were taken twice each season (during the period of main plant growth and shortly before harvest) under cultivation of sugar beet (2004) and winter wheat (2005). Within the study, CO_2-effects on abundance, diversity and stable C-isotopic signatures ($\delta^{13}C$) of collembolan species and nematode feeding types were analysed. As the stable C-isotopic analysis of taxonomically or functionally classified collembolans and nematodes represents a new research approach, influences of agents generally used during sample preparation on the $\delta^{13}C$ values of animals, and their applicability prior to stable C-isotopic analyses, were analysed.

The results reveal CO_2-enrichment induced changes of food availability and quality in the rhizosphere to affect the soil fauna in arable soil. In this context, modified microbial community compositions and activities, as well as changing quantities and qualities of exudates presumably represent the most important controlling factors. Intensity and manner of impacts, thereby, strongly depend on crop type and plant developmental stage and vary between species and functional groups of the soil fauna according to their food specificity and adaptability. Generally, stronger CO_2-effects under sugar beet compared to winter wheat cultivation, decreasing impacts with increasing trophic distances of organisms to primary producers, and stronger influences on specialists compared to generalists were detected. The results reveal the taxonomical and functional diversity of the soil fauna, and thus nutrient availability and finally soil fertility to change under future atmospheric CO_2-concentrations, depending on cultivated crop and season.

The present study provides insights into CO_2-enrichment induced alterations of C-translocation and interactions within the soil food web and, thus, in the context of climate change and agrobiodiversity conservation, contributes to improving knowledge of changes of below-ground processes, which are to be expected in the future.

Zusammenfassung

Im Rahmen der vorliegenden Dissertation wurde der Einfluss des atmosphärischen CO_2-Anstiegs auf die Collembolen- und Nematodengemeinschaft eines, unter Fruchtwechsel kultivierten, Agrarökosystems untersucht. Die Arbeit war Teil eines Freiland-CO_2-Anreicherungsversuchs nach dem FACE-Prinzip (Free Air Carbon Dioxide Enrichment), der auf dem Gelände des Johann Heinrich von Thünen Institutes (vTI) in Braunschweig durchgeführt wurde. Die Beprobungen erfolgten in den Jahren 2004 und 2005 unter Zuckerrüben- und Winterweizenanbau, jeweils während der Hauptwachstumsphase und kurz vor der Ernte der Kulturpflanzen. Analysiert wurde der CO_2-Effekt auf die Abundanz, die Diversität sowie die stabilen C-Isotopensignaturen ($\delta^{13}C$) der Collembolenarten und Ernährungstypen der Nematoden. Da die stabile C-Isotopenanalyse taxonomisch oder funktionell klassifizierter Collembolen und Nematoden einen neuen Forschungsansatz darstellte, wurden im Vorfeld der Untersuchungen verschiedene, praxisüblich bei der Probenaufbereitung verwendete Agenzien hinsichtlich ihres Einflusses auf die $\delta^{13}C$-Werte der Tiere, und somit hinsichtlich ihrer Anwendbarkeit im Rahmen von C-Isotopenanalysen untersucht.

Die vorliegenden Untersuchungen belegen, dass die Bodenfauna in Agrarökosystemen über CO_2-induzierte Veränderungen der Nahrungsverfügbarkeit und -qualität in der Rhizosphäre beeinflusst wird. Die Ergebnisse weisen darauf hin, dass Modifikationen der Zusammensetzung und Aktivität der mikrobiellen Gemeinschaft, sowie der Quantitäten und Qualitäten der Wurzelexsudate in diesem Zusammenhang die wichtigsten auslösenden Faktoren darstellen. Art und Intensität der Beeinflussung hängen stark von der Kulturpflanze und ihrem Entwicklungsstadium ab und variieren entsprechend der jeweiligen Ernährungsspezifität und Anpassungsfähigkeit zwischen verschiedenen Arten und funktionellen Gruppen der Bodenfauna. So wurde eine stärkere Beeinflussung unter Zuckerrüben-, verglichen mit Winterweizenanbau, eine Abnahme des CO_2-Effektes mit zunehmender trophischer Distanz der Organismen zu den Primärproduzenten und eine stärkere Beeinflussung von Spezialisten im Vergleich zu Generalisten nachgewiesen. Die Ergebnisse belegen, dass sich unter zukünftigen CO_2-Konzentrationen die taxonomische und funktionelle Diversität der Bodenfauna, und als Folge dessen auch die Nährstofffreisetzung und letztlich die Bodenfruchtbarkeit, in Abhängigkeit von der Kulturpflanze und ihrem Entwicklungsstadium ändert.

Die vorliegende Arbeit liefert Einblicke in CO_2-induzierte Veränderungen des C-Transportes und der Interaktionen innerhalb des Bodennahrungsnetzes und leistet somit im Kontext des Klimawandels und Agrobiodiversitätsschutzes einen wichtigen Beitrag zur Verbesserung des Kenntnisstandes hinsichtlich zukünftig zu erwartender Veränderungen von Bodenprozessen.

Part 1

1.1 Introduction

1.1.1 Climate change and atmospheric CO_2-enrichment

Atmospheric greenhouse gases (mainly: carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O), sulphur hexafluoride (SF6), hydrofluorocarbons (HFCs), and perfluorocarbons (PFCs)) sustain the average temperature on the earth's surface at a constant level of around 15 degrees Celsius by preventing the heat emitting from the earth from disappearing into space. This effect, referred to as natural greenhouse effect, establishes the basis for the development of all life on earth.

As a consequence of industrialization, the concentration of greenhouse gases, which originally accounted for only 3 ‰ of the total mass of the atmosphere, has risen strongly over the past 150 years. The radiation balance changes due to this rapid increase, whereby the atmosphere is heating up to an unnaturally high level. This non-natural anthropogenic greenhouse effect is continuously supported by industry, traffic, private households, agriculture, and land use changes. Thus, global anthropogenic greenhouse gas emissions increased by about 70 % from 1970 to 2004 (IPCC, 2007b).

Concerning this anthropogenic greenhouse effect, particular attention is directed to the steadily increasing share of carbon dioxide (CO_2), which is unavoidably released during fossil fuel burning. This enrichment of CO_2 in the atmosphere is additionally supported by the decline of the CO_2-sink capacity of terrestrial systems, which originally extracted about one third of combustion-released atmospheric CO_2 (Canadell et al., 2007). Consequently, global CO_2-emissions have risen by about 80 % from 1970 to 2004 (IPCC, 2007b). According to forecasts, if this trend continues atmospheric CO_2-concentrations will reach values of 450-500 $\mu mol\ mol^{-1}$ in about 50 years (IPCC, 2001), and of 500-1000 $\mu mol\ mol^{-1}$ at the end of the 21st century (Fung et al., 2005).

International measures for climate protection

As progressing climate changes are driven by global causes, a long-term trans-national cooperation and the division of responsibility between states are indispensable fundamentals to implement effective climate protection measures. To ensure internationally co-ordinated approaches, the United Nations Framework Convention on Climate Change (UNFCCC), an international, multilateral environmental protection agreement, was launched in 1992, as part of the “Agenda 21”, on the United Nations Conference on Environment and Development (UNCED) in Rio de Janeiro (UNFCCC, 1992). The ultimate objective of this convention is to achieve the stabilization of greenhouse gas concentrations in the atmosphere at a level that would prevent dangerous anthropogenic interference with the climate system. The time frame set to reach this level, should thereby allow the adaptation of ecosystems to climate change. This way, global warming should slow down, the consequences of climate change should be mitigated, and the maintenance of sufficient food production should be ensured.

The Framework Convention on Climate Change, which entered into force on March 21, 1994, establishes the basis for continuous international negotiation processes concerning climate protection. This political process is accompanied and assisted by the IPCC (Intergovernmental Panel on Climate Change) scientific committee.

A milestone in international climate policies is the Kyoto Protocol (UNFCCC, 1998), which was initially adapted for use on the third Conference of the Parties (COP 3) in 1997, and which entered into force on February 16, 2005 as an internationally binding agreement. The Kyoto Protocol establishes legally binding commitments, especially for the "Annex I" nations (mainly responsible industrialised countries), for the reduction of the emissions of the six most important greenhouse gases (CO_2, CH_4, N_2O, SF_6, HFCs, and PFCs) between 2008 and 2012 by 5.2 % against the 1990 level. Until January 2009, 184 Parties, which in total are responsible for 63.7 % of global greenhouse gas emissions, have ratified, acceded, approved or accepted the Protocol.

National measures for climate protection

Following the international climate protection efforts, Germany committed itself to reduce its CO_2-emissions by 25 % until 2005 compared to 1990 levels at the first conference of the parties in Berlin (1995). To attain this objective, the "National Climate Protection Programme of the Federal Republic of Germany" was adapted by the German government in the year 2000. This programme was elaborated, updated and finally followed by the valid "Climate Protection Programme 2005". As part of the EU burden-sharing under the Kyoto Protocol (UNFCCC, 1998), this programme commits to a 21 % reduction in German greenhouse gas emissions in the period 2008-2012 as compared to 1990 levels. For the same period, a joint reduction target for total CO_2-emissions was set at 844 million tonnes per year (BMU, 2005).

To develop and estimate possible adaptation measures, prospective studies were pursued to assess impacts of climate change on, for example, German agriculture (Schaller & Weigel, 2007), which is of major importance in the context of climate change (see Chapters 1.1.3 and 1.1.4). Since, nonetheless, up to now several uncertainties exist with regard to underlying climate-process relationships, there is still a need for research. In this context, the present study contributes to improving knowledge of CO_2-enrichment-induced changes of below-ground processes in arable soils.

1.1.2 Biodiversity in the context of climate change

The term “biodiversity” involves the diversity within species (genetic diversity), between species, and of ecosystems (CBD, 1992). Biodiversity is essential for maintaining life-sustaining systems of the biosphere, such as, for instance, the regulation of climate, water balance, or soil formation (BMELV, 2007). Moreover, several ecosystem functions, and hence services, directly depend on the biological diversity within systems (Naeem et al., 2007). Thus, the conservation of biodiversity is of utmost relevance to ensure the provision of numerous ecosystem services required by humans (BMELV, 2007).

Climatic changes, directly or indirectly, influence species distribution (Araújo & Rahbek, 2006), interactions between species (Emmerson et al., 2005, Tylianakis et al., 2008), their genetic constitution, and structures of ecosystems (Blankinship & Hungate, 2007; IPCC, 2007b). Thus, more sensitive species often have no possibility to elude climate-induced habitat changes, disruptions, or other global change-associated stressors, like, for example, land use changes or overexploitation of natural resources. According to the fourth assessment report of the IPCC (IPCC, 2007a), roughly 20-30 % of plant and animal species are expected to be at increased risk of extinction if global temperatures exceed 2 to 3°C above pre-industrial levels. As ecosystems represent functionally complex networks which show a strong interdependence between species, due to multitrophic interactions via food webs or element cycles (Tylianakis et al., 2008), the disappearance of a single species can involve the loss of others. Such substantial species losses have the potential to alter numerous ecosystem processes and functions, at worst resulting in the destabilization or disturbance of whole systems (Balmford & Bond, 2005; Emmerson et al., 2005).

In this context, highly specialized species which generally have more exacting metabolic or ecological requirements are considerably more vulnerable to habitat alterations than generalist species which are able to rapidly adjust themselves to changing conditions. Thus, distribution ranges and abundances of specialists would most probably decline under such scenarios, whereas generalists might profit and expand their ranges (Balmford & Bond, 2005). This selective removal of many sensitive, specialized, and often narrowly distributed species, coupled with increases in a small number of mostly cosmopolitan generalists, will lead to increased homogenization of biota (McKinney & Lockwood, 1999). Communities left behind will be more resilient and resistant to external anthropogenic impacts (Balmford, 1996), but, however, comprise a decreased functional diversity (McKinney & Lockwood, 1999). Considering that functional diversity refers to the diversity of species traits, and thus to ecosystem functioning and the services a system provides, rather than taxonomic diversity, in particular the conservation of functional biodiversity is crucial to maintain ecosystem processes (Blankinship & Hungate, 2007; Naeem et al., 2007).

Our ability to predict where, when, and by which and how much changes in wild nature and biodiversity human well-being will be affected is limited. Too few data even on current losses exist, our knowledge of the dynamics of future changes is incomplete (Balmford & Bond, 2005), and our understanding of the complex linkages between biodiversity of natural systems, its functions within natural regulation, and its relevance concerning service provision is as yet rudimentary (Tylianakis et al, 2008). Nevertheless, the available evidence clearly indicates that numerous threatened species, regions, and habitats are closely associated to the maintenance of frequent human-required ecosystem services (Tylianakis et al., 2008). Consequently, predicted future losses of natural resources will corrupt human well-being considerably (Balmford & Bond, 2005). Thus, the sustainable conservation of biodiversity is of great importance, particularly in view of progressing climate change.

International measures for biodiversity protection

Two major international initiatives were launched in recent years to detect changing states of various ecosystems and their biodiversity; to assess consequential effects on human society and human welfare which are currently less understood (Balmford & Bond, 2005); to develop appropriate measures, and, thus, to guarantee the world-wide protection of biodiversity. The "Convention on Biological Diversity" (CBD) (CBD, 1992), which was adopted at the United Nations Conference on Environment and Development (Earth Summit) in Rio de Janeiro in 1992, and the "Millennium Ecosystem Assessment" (Millennium Ecosystem Assessment 2004), launched in June 2001, both strive to achieve these goals.

The three central targets of the CBD, which was signed by 190 parties and the European Community, and which entered into force in 1993, are to conserve biodiversity, to enhance its sustainable use, and to ensure an equitable sharing of benefits linked to the exploitation of genetic resources (CBD, 1992). In this context the CBD addresses both in-situ conservation, which focuses on conserving genes, species, and ecosystems in their natural surroundings, and ex-situ conservation, defined as the conservation of components of biological diversity outside their natural habitats, for example by means of gene banks or botanic gardens.

Moreover, existing uses, like agriculture or forestry, must comply with the sustainability principle (CBD, 1992). In September 2002, at the Johannesburg World Summit on Sustainable Development, representatives of 190 countries committed themselves to achieve a significant reduction of the current rate of biodiversity loss at the global, regional and national scale by 2010 ("2010 Biodiversity Target") (CBD, 2007). According to the UNEP (2002), this commitment represents a contribution to poverty alleviation and to the benefit of all life on earth, the central target of the CBD.

The Millennium Ecosystem Assessment (MA) (Millennium Ecosystem Assessment, 2004) bases on the cooperation of a large and diverse suite of natural and social scientists. Like the Intergovernmental Panel on Climate Change (IPCC), the MA assesses current knowledge, scientific literature, and data. It aims to provide decision makers and the public with a broad scientific evaluation of the consequences of current and projected ecosystem changes concerning human society and human well-being (Naeem et al., 2007), and, moreover, gives advice on political approaches for encountering those changes (Millennium Ecosystem Assessment, 2004). The MA, which is working at multiple scales from local to global, was established to meet the needs of already existing international conventions like the CBD, the "United Nations Convention to Combat Desertification" (UNCCD) which entered into force in 1996, and the "Ramsar Convention on Wetlands" (Balmford & Bond, 2005).

For the inner-European implementation of the CBD a "Biodiversity Action Plan" (European Commission, 2001a) was developed in 2001. This plan includes four central targets: (1) to conserve biological diversity within the European Union; (2) to protect global biodiversity; (3) to support the adaptation of biodiversity to climate change; and (4) to improve the knowledge base for conservation and sustainable use of biodiversity in the EU and globally.

During the "EU Summit" in Göteborg 2001, the EU heads of governments, moreover, committed themselves to halting the loss of biodiversity by 2010, according to the "2010 Biodiversity Target" of the CBD.

National measures for biodiversity protection

Concerning the loss of biodiversity in Germany, in particular the threat to species (increased probability of extinction) and the impairment or destruction of habitats represent major problems. In this context, intensive land use in agriculture; the discontinued agricultural use of ecologically valuable marginal land; the direct destruction and dissection of habitats; discharge of pollutants and nutrients; local deficits in forest management; leisure uses which have an adverse impact on nature; non-sustainable fishing practices; increased proportions of invasive non-native species; and, not least, climate change, represent the main threats to biodiversity in Germany (BMU, 2007). To counteract these stressors, to guarantee the sustainable use of nature, and to protect biodiversity, the Federal Ministry for the Environment, Nature Conservation and Nuclear Safety (BMU) developed the "National Strategy on Biological Diversity" (BMU, 2007), which was adopted by the Federal Cabinet in November 2007. This comprehensive strategy specifies 330 quality targets and action objectives for all biodiversity-related topics and, moreover, involves about 430 measures for biodiversity protection. It fulfils Germany's obligations under Article 6 of the CBD (CBD, 1992), which states that "each contracting party shall develop national strategies, plans or programmes for the conservation and sustainable use of biological diversity or adapt for this purpose its existing strategies, plans or programmes" (BMU, 2007). The strategy serves to implement the CBD at the national level, and is targeted at the mobilization of all social forces with the aim of significantly minimizing and then halting the threat to biological diversity in Germany. Ultimately the current trend should be reversed in favour of an increase in biological diversity, including its typical regional peculiarities. In the overall strategy, equal consideration is given to ecological, economic and social aspects in keeping with the guiding principle of sustainability. Deadlines to achieve all strategies targets range from the immediate term through to the year 2050.

Furthermore, a system of indicators for assessing the impacts of climate change on biological diversity should be formulated and established by 2015 (BMU, 2007).

1.1.3 Key-role of agrobiodiversity in the context of climate change

Globally, approximately 28 % of the total land area (Nösberg & Long, 2006), and nearly 103 million ha land within the European Union (FAO-STAT, 2005; cit. ex Henle et al. (2008)), are covered by agroecosystems. These agricultural landscapes ensure the supply of food, wood, fibre, and renewable energy (Nösberg & Long, 2006), and, therefore, play a major role in human well-being. Moreover, these regions are of importance in the context of climate change as they account for 26-28 % of all terrestrial carbon storage (Nösberg & Long, 2006), contribute to the cycling of carbon, water, and nutrients on a continental scale (Weigel et al., 2006), and feedback on climate by means of land management-induced (fertilization, irrigation, tillage etc.) changes of physical land surfaces and biogeochemical cycles (e.g., Ogle et al., 2005).

Due to this broad range of functions, the protection of the biological diversity of these regions, which is referred to as agrobiodiversity, is relevant to the provision and performance of services essential to human survival. With regard to future food demands, which require increasing agricultural production to prospectively ensure food security for the continuously rising global population (Ingram et al., 2008), this importance is even likely to increase in future. As the adaptation of systems to altering conditions, like those expected, and to some extent already noticeable, under climate change, directly depends on a large species and gene pool (Loreau et al., 2001), the conservation and maintenance of agrobiodiversity is essential to ensure future human welfare.

Agrobiodiversity in this context is defined as the diversity in life forms used or able to be used directly or indirectly by humankind, in efforts to secure the resources vital to survival (BMELV, 2007). According to this definition, agrobiodiversity includes species- and genetic diversity of life forms whose preservation is directly linked to the implementation of basic human needs, like for example crops or livestock. Moreover, the biodiversity associated with these organisms that fulfils various utilization-relevant functions, is involved as well. This associated biodiversity is of major importance since the provision of services by most directly usable organisms strongly depends on their interspecific interactions and on the multifaceted functions of respective ecosystems. Thus, for instance, insects, which play a major role concerning pollination processes, or soil organisms (soil fauna and soil microorganisms), which directly influence soil fertility, represent crucial constituents of agrobiodiversity as well (BMELV, 2007).

The present study, which focuses on CO_2-enrichment effects on the soil fauna in arable soil (Papers 2.1, 2.2 and 2.3), therefore, contributes to supporting efforts on agrobiodiversity conservation by improving the understanding of future below-ground processes, necessary to develop appropriate future management measures.

International measures for agrobiodiversity protection

In the face of climate change and future global food demands, the conservation of agrobiodiversity represents a substantial aim of the CBD and an important aspect of the “2010 Biodiversity Target” (CBD, 2007). Thus, the Conference of the Parties of the CBD adopted a programme of work on agricultural biodiversity in 2000 (CBD, 2000). This programme consists of four elements (assessment, adaptive management, capacity-building, and mainstreaming) and three cross-cutting initiatives (on pollinators, soil biodiversity and biodiversity for food and nutrition).

European-wide programs have been developed and laws have been passed in order to protect and conserve the biodiversity of arable landscapes (Henle et al., 2008). In this context, the "Biodiversity Action Plan for Agriculture" (European Commission, 2001b) was adopted by the European commission in 2001 under the Common Agricultural Policy of the European Union (CAP). This Action Plan complements the "Agri-Environmental Strategy", which is largely aimed at enhancing the sustainability of agro-ecosystems.

National measures for agrobiodiversity protection

In addition to the "National Strategy on Biological Diversity" (BMU, 2007), the German Federal Ministry of Food, Agriculture and Consumer Protection (BMELV) published the strategy "Conservation of Agricultural Biodiversity, Development and Sustainable Use of its Potentials in Agriculture, Forestry and Fisheries" in December 2007. The main targets of this strategy are to achieve a long-term conservation and a broader-based use of genetic resources; to achieve the sustainable use of agricultural biodiversity while protecting natural ecosystems and threatened species; to strengthen the international cooperation; and to achieve a globally coordinated strategy for the management of global resources (BMELV, 2007). Thereby, this strategy mainly focuses on the conservation of biodiversity which is directly or indirectly used for food, agriculture, forestry and fisheries.

Beside the conservation of these species and their genetic diversity, the strategy pursued the target of ensuring the sustainable use of agricultural systems, thereby contributing to the implementation of "Germany's Sustainability Strategy".

1.1.4 Agroecosystems under atmospheric CO_2-enrichment

Cultivated crops and crop yield

Agroecosystems, cultivated plants, and all agricultural production are directly and indirectly affected by climate change via rising temperatures, changing precipitation regimes, and increasing atmospheric CO_2-levels (IPCC, 2007a). Higher temperatures, for example, induce grain yield losses, mainly by shortening the life-cycle of crops and speeding the rate of development through grain-filling (Porter et al., 2007). Elevated atmospheric CO_2-concentrations, in contrast, stimulate photosynthesis (sugar beet: 45 %; winter wheat: 37 %) (Weigel et al., 2005; Ainsworth & Rogers, 2007), enhance growth and yield ("CO_2

fertilization effect”), and reduce canopy evapotranspiration (sugar beet: 21 %; winter wheat: 6 %) whereby the water-use efficiency is improved (Weigel et al., 2005). Moreover, CO_2-enrichment increases the total biomass production above- and below-ground (Weigel, 2005), changes rhizodeposition processes (Phillips et al., 2006b), and enhances the C-allocation to roots (Weigel, 2005) as well as the use efficiency of light and nitrogen (N) (Dijkstra et al., 2008). The structure of standing crops changes due to altered leaf area indices and accelerated branching (Weigel, 2005).

As our understanding of underlying factors and processes, causing the broad variability of CO_2-enrichment-induced crop responses, is as yet rudimentary, the consequences of climate change on the availability and nutritional quality of numerous foods have been uncertain up to now (Porter, 2007). In order to close existing gaps in knowledge, it is necessary to more strongly include ecosystem components others than cultivated crops, which received the most attention during previous studies. Such constituents might be of importance as they are affected by increasing atmospheric CO_2-concentrations as well and, moreover, have the potential to influence crops and yields via feedback effects and interactions.

In this context, soils and soil food webs, which are actively involved in decomposition processes and closely connected to nutrient availability, are of utmost relevance (Drigo et al., 2008; Pendall et al., 2008). As compositions of soil food webs strongly depend on plant species, the structure of their root systems, and their age (e.g., Yeates & Bongers, 1999), potential soil organism-mediated feedback effects on crops and yields might vary as well, depending on these factors. Accordingly, the inclusion of various crop types and plant growth stages is essential when investigating and assessing CO_2-effects on soil processes in agroecosystems.

Following this requirement, two morphologically and metabolically differing crop types (sugar beet and winter wheat) and, moreover, two plant developmental stages, were included in the present study (Papers 2.2 and 2.3), in order to analyse and consider potential crop-dependences of below-ground CO_2-effects.

Soil and soil food webs

Soils, which store about 70 % of total terrestrial carbon (C), play a major role in the C-cycle of ecosystems and the nutrient supply to plants (Pendall et al., 2008). Due to photosynthetic CO_2-fixation, CO_2-release through respiration, sequestration of C into biomass and soil, and organic matter decomposition by soil organisms, a continuous C-exchange (direct and indirect) exists between soils and atmosphere (Drigo et al., 2008). Globally, the above- to below-ground C-transport in terrestrial ecosystems is of enormous magnitude and by far exceeds the C-emissions to the atmosphere through combustion of fossil fuels (Litton & Giardina, 2008). Although these top-down C-fluxes influence biological, chemical and physical properties of soils and ecosystems to a vast extent via the regulation of C-storage and decomposition processes, so far they remain minor investigated and understood (Litton & Giardina, 2008). Thus, distinct results and precise details of CO_2-enrichment-induced changes hardly exist (Litton & Giardina, 2008).

However, since 80-90 % of plant-fixed C finally reaches the soil decomposer community (Bardgett et al., 2005), it must be assumed that the C-transport into and within the soil and, thereby, soil habitat properties and conditions change as well under atmospheric CO_2-enrichment. In this context, in particular CO_2-enrichment-induced changes of quantities and qualities of root exudates, along with altered microbial activities (Drigo et al., 2008; Haase et al., 2008), both representing important food sources of the soil fauna (Pollierer et al., 2007; Drigo et al., 2008), might most probably affect the decomposer community via the soil food web (Pendall et al., 2008). Since various soil fauna groups and embedded species differ among each other concerning their adaptation levels to certain habitat conditions, which determine their occurrences and abundances (Balmford & Bond, 2005), such impacts have the potential to alter population densities, species compositions, and interactions within soil food webs, and thus the functional diversity of soils (Tylianakis et al, 2008). This way, nutrient release, soil fertility, and finally, cropping capacity and productivity of soils, might inevitably change as well (Brussaard et al., 2007).

Thus, structural-, trophic- and functional alterations within soil fauna communities provide possible causes of the broad variability of CO_2-induced crop responses (Phillips et al., 2006a). However, globally and regional, at the functional and taxonomical level, up to now, less is known concerning species becoming extinct, population decreases (Balmford & Bond, 2005), and changes of functional networks in soil resulting thereof. A lack of knowledge exists particularly with regard to key-organisms in soil.

Thus, studies of CO_2-enrichment effects focusing on functional aspects of various trophic levels and interactions within soil food webs represent a missing link in the quantification of CO_2-effects on numerous ecosystem services (Tylianakis et al., 2008), like future yield levels. Against the background of increasing food demands, decreasing availability of production areas, the required conservation of natural resources, and, moreover the protection of soil biodiversity which represents a crucial aspect of the programme of work on agricultural biodiversity of the CBD (CBD, 2000), an urgent need for research exists.

Based on this state of knowledge, impacts of atmospheric CO_2-enrichment on the taxonomic or trophic and functional diversity of collembolans and nematodes, which represent key-organisms within the soil fauna of arable soils (Freckman & Ettema, 1993; Petersen, 2000) and thus contribute to agrobiodiversity (CBD, 2000; BMELV, 2007), were investigated in the present study (Papers 2.2 and 2.3). The results should give insights into, up to now, barely understood links and relations within and between modified C-translocation processes and complex interactions within soil food webs under future conditions. Since predictions of future distributions of species from bioclimatic models may fail due to uncertain predictions of local climate changes, inaccurate estimates of the climatic tolerance of species, and unforeseen changes in populations (Araújo & Rahbek, 2006) field experiments were necessary within the scope of the present study.

1.1.5 The FACE field experiment

To meet the need of research concerning impacts of atmospheric CO_2-enrichment on ecosystem processes, FACE (**F**ree **A**ir **C**arbon **D**ioxide **E**nrichment) field experiments have been established in various ecosystems all over the world (FACE Data Management System, 2009). This technology, applied since the late Eighties (Hendrey et al., 1992), allows the study of the impacts of future atmospheric CO_2-concentrations on several components of different ecosystems under natural conditions, with a practical orientation and without chamber effects (Nösberg & Long, 2006). Unique in Europe, the Johann Heinrich von Thünen Institute (vTI), Federal Research Institute for Rural Areas, Forestry and Fisheries (formerly Federal Agricultural Research Centre, FAL) in Braunschweig ran such field experiment from 1999 until 2005 within an agroecosystem managed in a crop rotation (Weigel et al., 2006). The rotation cycle was repeated once during the total duration of the CO_2-exposure experiment. The present study was part of this experiment and was conducted under cultivation of sugar beet as a root crop and winter wheat as a cereal crop in the years 2004 and 2005, during the second crop rotation cycle within the experiment. Both crop types were chosen to investigate CO_2-effects on below-ground processes, as they differ markedly in terms of their root systems, which regulate and influence community compositions within the soil food web, and thus the functional diversity and interactions in soils. Moreover, impacts under sugar beet and winter wheat cultivation are of particular interest since both crops belong to the most common and economically important field crops.

Site description – experimental field

The FACE-equipment was established in a 22-ha field located at the vTI site in Braunschweig, south-east Lower Saxony, Germany (52° 18' N, 10 ° 26' O, 79 m a.s.l.). The local climate is characterized by a mean annual temperature of 8.8°C, a total precipitation of 618 mm $year^{-1}$, 1514 h sunshine $year^{-1}$, and a solar radiation of approximately 350 kJ cm^{-2} $year^{-1}$ (Weigel et al., 2005). The soil at the experimental site is a Luvisol of a loamy sand texture with a pH of 6.5 and a mean organic carbon content of 1.4 %.

The field was managed in a locally typical crop rotation including winter barley (*Hordeum vulgare* cv. Theresa), ryegrass as a cover crop (*Lolium multiflorum* cv. Lippstädter Futtertrio), sugar beet (*Beta vulgaris* cv. Impuls), and winter wheat (*Triticum aestivum* cv. Batis). To avoid water stress, field irrigation was applied during the main growing season (Weigel et al., 2005). Soil-, fertilizer-, and pesticide management measures were carried out according to local farming practices. Crop varieties, CO_2-treatment details, and sampling dates under sugar beet cultivation 2004 and winter wheat cultivation 2005, when samples for the present study were taken, are briefly summarized in Table 1.

Table 1: Crop developmental stages as well as treatment and sampling dates under sugar beet (2004) and winter wheat (2005) cultivation in the FACE experiment in Braunschweig (Table 1, cit ex. Paper 2.2)

Management	**Sugar beet 2004** *Beta vulgaris* cv. "Impuls"	**Winter wheat 2005** *Triticum aestivum* cv. "Batis"
Crop		
Sowing	14 April 2004	26 October 2004
Emergence	26 April 2004	16 November 2004
Final harvest	15 October 2004	27 July 2005
Atmospheric CO_2-enrichment		
Start	14 May 2004	12 January 2005
End	30 September 2004	20 July 2005
Duration	139 days	130 days
Mean CO_2-concentration (Control vs. FACE)	378 vs. 549 ppm	377 vs. 549 ppm
Sampling		
First sampling (t1)	21 June 2004	10 May 2005
plant principal growth stage[1)]	1: Leaf development (BBCH15)	4: Booting (BBCH41)
Second sampling (t2)	21 September 2004	25 July 2005
plant principal growth stage[1)]	3: Rosette growth (BBCH38)	8: Ripening (BBCH89)

[1)] Plant growth stages following the BBCH scale of Meier (2001)

Atmospheric CO_2-enrichment via FACE technique

The FACE equipment consisted of six circular plots (rings) of 20 m diameter, engineered by the Brookhaven National Laboratory New York, USA (Hendrey et al., 1992; Lewin et al., 1992). Each plot was surrounded by 32 vertical vent pipes with several holes facing the inside of the plots. The standing pipes were attached to control valves located at their bases that were all connected to a wide ring-shaped pipe called a plenum. The plenum connected to a blower and instrument shelter. The blower forced air into the plenum, where the air circulated. By opening or closing the computer-regulated pneumatic control valves, quantities and placement of air injection into ring plots via passing the holes of the vent pipes was regulated. To ensure an equal distribution of air across the rings, the supply was regulated depending on wind direction and speed, which were digitally analysed by sensors located in the centres of the rings.

Two of the six rings which were set up in Braunschweig were control rings, wherein unchanged ambient air, with a CO_2-concentration of about 360 ppm, was blown into the standing crop.

Two further rings were treated with air which was enriched in carbon dioxide by adding tank-derived CO_2. The target CO_2-concentration of the air within these FACE rings was about 550 ppm, corresponding to the atmospheric CO_2-level expected to be reached in 2050 (IPCC, 2001). To maintain this CO_2-concentration at a constant level it was regularly monitored by gas analysers located in the middle of both FACE rings, which were directly linked to the computer system regulating the CO_2-supply from the tank. Moreover, the spatial distribution of CO_2 across the area inside the rings was recorded and controlled by a two-level gas sampling system.

Fumigation of FACE and control rings was conducted only during daylight hours and was stopped when wind speeds exceeded 6.5 m s^{-1}. As low air temperatures induce a reduction of plant physiological activities, and thus of the photosynthetic CO_2-fixation, fumigation was also interrupted when air temperatures dropped below 5°C.

The final two rings of the field experiment represented ring dummies which were equipped with the same devices as FACE and control rings, but contained no blowers. These rings were installed at the beginning of the experiment in 1999 to analyse potential equipment effects. As no such effects were detected during the total duration of the FACE experiment, these rings were not considered during the present study. Thus, all presented results refer to control and FACE treatments.

Beside both CO_2-levels, the Braunschweig FACE experiment included two nitrogen (N) fertilization levels (adequate N-fertilization vs. low (50 % of adequate) N-fertilization) in order to simulate future nutrient management scenarios and to analyse potential C-N interaction effects.

Since previous studies reveal the soil fauna to be not affected by CO_2-elevation-N-fertilization interactions (Sticht et al., 2006) only adequately fertilized areas were considered during the present study.

Stable isotopic labelling of surplus CO_2

Within the Braunschweig FACE experiment, isotopically labelled CO_2 was used to simulate atmospheric CO_2-enrichment. Compared to ambient carbon dioxide, the tank-derived CO_2 was depleted in the heavier ^{13}C isotope, resulting in a more negative $^{13}C/^{12}C$ ratio (stable C-isotopic signature expressed as $\delta^{13}C$) of -47 ‰. By mixing this labelled CO_2 with unchanged ambient air, a decrease of $\delta^{13}C$ was induced from an initial value of -9.85 ‰ of the air within the control to about -21 ‰ of the CO_2-enriched air within the FACE rings. This isotopic labelling allowed tracing of the surplus C, added during CO_2-enrichment, in different compartments of the system (crops, soil, nematodes and collembolans) by means of stable C-isotopic analyses. The experimental set-up, therefore, provided a unique opportunity to gain new insights into C-translocation processes, interactions, and trophic shifts within the soil food web under future atmospheric CO_2-conditions.

As the stable C-isotopic analysis of field-sampled nematodes (subdivided into feeding types), and collembolans (classified to species level), represented a new research approach, some preliminary methodical tests were required. In this context an appropriate weight of nematode samples, and therefore a well measurable number of individuals, allowing the precise analyses of animal $\delta^{13}C$ values, had to be determined. Concerning the taxonomical or trophic classification of soil fauna, the preservation and fixation of animals, or, when determined at the species level, moreover, bleaching of organisms is often indispensable. The agents commonly used for this purpose usually represent C-sources which have the potential to modify $\delta^{13}C$ values of species tissues. Generally only less literature was available concerning this methodical problem, and existing publications focussed solely on the preservation of aquatic organisms, various tissues of birds and mammals, or documented investigations of *Drosophila melanogaster* (e.g., Arrington & Winemiller, 2002). Only insufficient knowledge existed on whether and in which way the treatment with such agents alters the $^{13}C/^{12}C$ ratio of soil animals. Thus, prior to field samplings, effects of several chemical agents customarily used during sample preparation of collembolans and nematodes on the $\delta^{13}C$ values of these organisms were determined, in order to detect under which conditions which agents are suitable prior to stable C-isotopic analysis of soil animals (Paper 2.1).

1.1.6 Soil fauna

According to the body size of organisms, the soil fauna is subdivided into three groups: macrofauna (> 2 mm diameter; e.g., earthworms or myriapodes); mesofauna (100 µm to 2 mm diameter; collembolans, mites etc.); and microfauna (< 100 µm diameter; e.g., nematodes or protozoans) (Swift et al., 1979). Concerning the soil animals analysed during the present study, collembolans represent keystone organisms of the meso- , nematodes of the microfauna.

Collembolans (Arthropoda, Hexapoda)

World wide approximately 7500 collembolan (springtail) species out of 74 genera, whereof about 2000 occur in Central Europe, have been described up to now (Bellinger et al., 1996-2008). Nearly all terrestrial habitats, in the first place the soil, were inhabited by collembolans often in high abundances (Hopkin, 1997).

Despite their small body size of 1-5 mm (in exceptional cases 0.12-17 mm) (Bellinger et al., 1996-2008), collembolans, as important members of the decomposer community, are of major relevance concerning soil nutrient availability as they catalyze nutrient mobilisation and increase microbial activity by grazing on bacteria and fungi (Petersen, 2000; Kaneda & Kaneko, 2008). Particularly with regard to agricultural soils, which often inhabit very high individual densities of collembolans, they play a key role concerning C-cycling and nutrient supply to crops (Hopkin, 1997; Petersen, 2000).

Collembolans are able to use a broad range of various food sources, as for example decomposed plant material, root exudates, fungal spores and hyphae, bacteria, algae, pollen, or diatoms (Berg et al., 2004), but are to a variable extent selective in their food choice (Bracht Jørgensen et al., 2008; Larsen et al., 2008). Preferences for certain food sources thereby differ depending on age, species (Bracht Jørgensen et al., 2008), habitat (Castaño-Meneses et al., 2004), seasonal variations (Berg et al., 2004), quality of food sources (Bracht Jørgensen et al., 2008; Larsen et al., 2008), and inhabited soil layers (Hishi et al., 2007).

According to their vertical stratification, collembolans can be subdivided into three life strategy forms, based on the classification of Gisin (1943). According to this classification, species that inhabit deeper soil layers are referred to as “euedaphic”, those occurring in the upper soil layer as “hemiedaphic” species. Surface-dwelling “atmobiont” species, living either on the soil surface or on macrophytes, represent the third life form type. As atmobiont species are of subordinate importance with regard to intra-soil processes, they were not considered during analyses of CO_2-enrichment-induced functional changes of soil processes during the present study. Concerning these changes, the attention was directed to euedaphic and hemiedaphic collembolan species (Paper 2.2), which differ markedly in terms of morphological and functional properties (Gisin, 1943). Morphological adaptations, in this context, are the result of a decrease in pore volume and the reduction of light with increasing soil depth. Whereas euedaphic species are generally characterized to be photophobic and drought-sensitive, the hemiedaphic life strategy involves xero-, meso-, and hydrophilous species. As a result of these different adaptabilities and sensitivities, collembolans respond differently to changing habitat conditions depending on respective life strategy and species.

According to the combination of these characteristics, accompanied by high species diversities, short generation times, and a close habitat-linkage due to their low mobility (Ehrnsberger, 1993), collembolans represent valuable biological indicators for assessing anthropogenic impacts on various ecosystems (Ehrnsberger, 1993; Parisi et al., 2005).

Nematodes

Nematodes (roundworms) inhabit all conceivable aquatic and terrestrial habitats, and, according to Bongers & Schouten (1991), account for up to 80 % of all metazoans on earth. Free-living nematodes include about 11,000 described species (Andrassy, 1991), reach body lengths of between 0.3 and 5.0 mm in soil (Yeates & Bongers, 1999), and inhabit most soils (Hoeksema et al., 2000) in often high abundances of up to 10 million individuals m^{-2} (Dunger, 1983). Thus, nematodes, which account for about 5 % of the total soil biomass, behind protozoa, represent the most abundant animals in soils (Gisi, 1997).

Nematodes are mainly characterized by a high trophic diversity between species. Thus, soil nematode communities involve herbivorous, bacterivorous, fungivorous, and predacious as well as omnivorous feeding types, which moreover differ concerning their functional roles in soil systems (Yeates, 2003). With regard to soil decomposition processes, the large group of non-phytopathogenic nematodes is of major importance. Microbial biomass and activity, and thereby C- and N-turnover as well as nutrient availability in soils are directly regulated by the grazing activity of bacterivorous and fungivorous nematodes (e.g., Liang et al., 2005), and indirectly affected by the regulation of root exudation through herbivorous nematodes (e.g., Poll et al., 2007). This way, nematodes contribute considerably to fundamental ecological processes in soil, as they regulate both primary production and decomposition processes.

According to these characteristics along with high species numbers, high abundances, short generation times, a high degree of food specialization, and their immediate responses to changing habitat conditions, nematodes species and feeding types offer great potential for use as indicators of biodiversity (Yeates & Bongers, 1999), and for assessing anthropogenic functional changes in various ecosystems (Hoeksema et al., 2000; Yeates, 2003).

Since nematodes, especially herbi-, bacteri- and fungivorous species (Freckman & Ettema, 1993), occur in high individual densities in arable soils (> $100g^{-1}$ soil) (Young et al., 1998), they represent valuable indicator organisms for analysing CO_2-effects on below-ground processes and functional links in agroecosystems as well. The separation of nematode feeding types, in this context, provides insights in impacts on different trophic levels of the soil food web and allows conclusions on changes within the microbial community.

Against this background, collembolans and nematodes were used as indicator-organisms to quantify CO_2-effects on the soil food web and soil processes in an agroecosystem, within the present study (Papers 2.2 and 2.3).

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1.2 Hypothesis and aims of the thesis

Overall hypothesis of the thesis:

Atmospheric CO_2-enrichment induces changes in taxonomic and functional diversity of the soil fauna in agroecosystems through quantitatively and qualitatively changed C-inputs into the soil.

Aims of the thesis:

- to develop sample preparation methods that allow the taxonomic or functional classification of collembolans and nematodes prior to analyses of their stable C-isotopic signatures; to detect impacts of commonly used agents on soil animal δ^{13}C-values; and to assess the expressiveness of animal stable C-isotopic signatures

- to gain insights into currently less understood CO_2-enrichment-induced changes within the soil food web and the C-cycle of an agroecosystem by combining analyses of biodiversity and stable C-isotopic signatures of functionally different groups of collembolans and nematodes; and to assess to which extent this new integrated research approach provides insights into impacts on soil processes

- to trace driving forces regulating CO_2-effects on various functionally and trophically differing soil fauna groups in arable soils, by means of relative abundances and stable C-isotopic signatures of animals (collembolans and nematodes), soil, and selected plant parts; and to analyse whether impacts differ between root and cereal crops

- to detect whether CO_2-effects on soil fauna communities differ depending on crop developmental stage

The present study contributes to improving knowledge of CO_2-enrichment effects on agrobiodiversity and C-turnover processes in arable soils, which are of major importance for the development of appropriate management measures to promote the adaptation of agriculture to climate change.

Part 2

2.1 Influence of chemical agents commonly used for soil fauna investigations on the stable C-isotopic signature of soil animals