Management practices for agricultural peat preservation in the face of climate change

By:

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General Abstract

Agricultural peatlands of the UK are highly productive, yet risk increased rates of degradation due to drainage and the climate change. The purpose of this body of work is to 1) fill knowledge gaps concerning the effects of the climate change on the Carbon cycle and horticultural production of agriculturally-utilised peatlands; 2) advise farmers on the suitability of increasing the field water table as a means of peat preservation.

The research examines: 1) the influence of 2°C and 5°C warming on greenhouse gas emissions and DOC production from agricultural peat; 2) the effects of 2°C and 5°C warming and atmospheric CO_2 concentration of 850 ppm on yield of radish, celery and romaine lettuce; 3) the effects of raising the water table from the field level of -50 cm to -40 cm and -30 cm on greenhouse gas emissions; 4) whether increasing the water table from the field level of -50 cm to -40 cm and -30 cm would constrain or improve yields of radish, celery and romaine lettuce.

The results suggest that the future global warming in the UK will cause higher rates of peat loss and varying effects on horticultural production on peat. It is not easy to explain the lower plant biomass in conditions of elevated atmospheric CO_2, however, it may be related to waterlogging and insufficient nutrient uptake from peat. Raising the water table would preserve agricultural peats for longer and lower emissions of carbon dioxide, however, this would happen at the expense of yield and increased DOC production. The emissions of methane were generally low or negative, even at higher water table levels, which shows that raising the water table to -30 cm or -40 cm would result in overall lower radiative forcing.

Author's declaration

I, Magdalena Justyna Matysek, declare that all the material contained within this thesis is a result of my own work and has been written by myself. This submission has not previously been presented for an award at this or any other institution. The research has been funded by the Grantham Centre for Sustainable Futures.

Publications arising from this thesis:

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In preparation for publication. Presented as Chapter 4.

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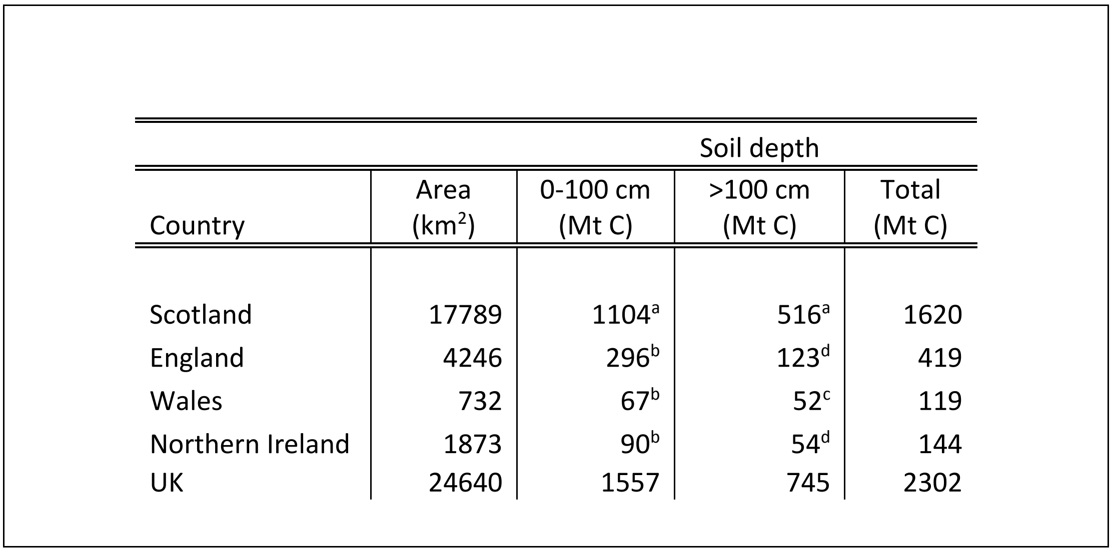
General Introduction

1.1 Peatlands as repositories of organic carbon

Soil organic carbon (SOC) is a component of soil organic matter (SOM). The percentage content of SOC in SOM is typically between 50 to 60%, although there may be significant variations between various soils (Rodeghiero et al., 2009). Globally, soils are the second largest storage of C (the largest one being oceans) and contain approximately 1500 Gt C (Zimov et al., 2006). Peatlands alone store 550 Gt C (which is 30% of SOC worldwide) (Parish et al., 2008). This means that one-third of the total SOC is contained in peat despite peatlands covering only 3% of terrestrial lands (Rydin and Jeglum, 2006). Peatlands cover 15% of the land area in the UK and store around 2300 Mt C (Billett et al., 2010) (Fig. 1.1).



		Soil depth		
Country	Area (km^2)	0-100 cm (Mt C)	>100 cm (Mt C)	Total (Mt C)
Scotland	17789	1104[a]	516[a]	1620
England	4246	296[b]	123[d]	419
Wales	732	67[b]	52[c]	119
Northern Ireland	1873	90[b]	54[d]	144
UK	24640	1557	745	2302

Figure 1.1: Area and C storage of peatlands in the UK. [a]Chapman et al. (2009); [b]Bradley et al. (2005); [c]Smith et al. (2007); [d]Pro rata to Scottish stocks below 1 m.

Source: Billet et al., 2010

In the UK, an organic soil is classified as peat if it meets two conditions: 1. the peat layer must be at least 40 cm thick; 2. the peat layer must not be buried by a mineral layer thicker than 30 cm (Holman and Kechavarzi, 2011). Peatlands are created when the rate of biomass accumulation is higher than the rate of organic matter mineralisation: such conditions are present under anoxic conditions (Rydin and Jeglum, 2006). Once a peatland is drained, the peat surface undergoes wastage as time goes by: the continued existence of peatlands depends on maintenance of waterlogging (Parish et al., 2008). Peat wastage is the outcome of three processes: consolidation, oxidation and shrinkage of peat (Holman and Kechavarzi, 2011) (Fig. 1.2). Consolidation involves peat compression, which is a result of increased surface pressure once soil buoyancy is reduced with a falling water table; whereas oxidation and shrinkage involve decreases in peat volume as a consequence of decomposition and desiccation, respectively (Wösten et al., 1997). The processes of consolidation and shrinkage do not lead to losses of SOM and SOC, unlike peat oxidation (Page et al., 2011). Additionally, peat wastage is exacerbated by wind erosion, burning and removal of soil during harvest (Holman and Kechavarzi, 2011). The majority of microbial decomposers in soil require oxic conditions to perform metabolic processes: anaerobiosis as a result of flooding constrains their activity, consequently preventing mineralisation of SOM (Page et al., 2011). Organic C may be lost from peat as either dissolved organic carbon (DOC), with wind and water erosion as particulate organic carbon (POC), or as greenhouse gases (GHG): carbon dioxide (CO_2) and methane (CH_4) (Fig. 1.2). Global warming could affect peatland ecosystems, contributing to greater SOC loss and creating a positive warming feedback through enhanced emissions of CO_2 (Billett et al., 2010; IPCC, 2014).

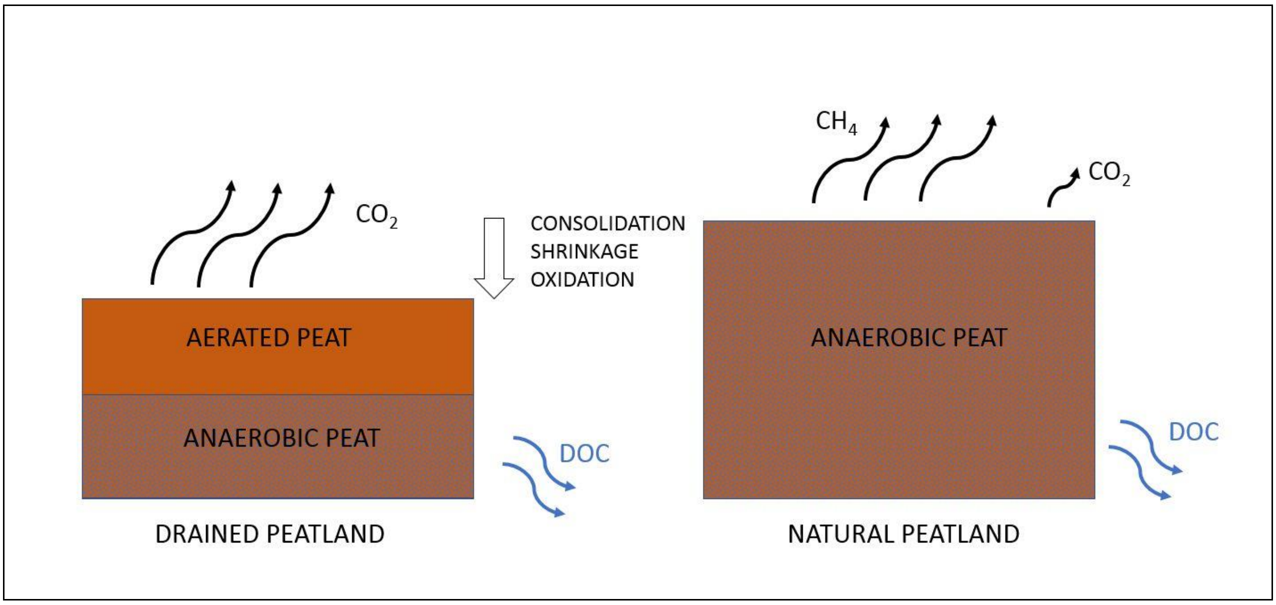


Figure 1.2: Effects of drainage on peat properties and C loss. DOC – dissolved organic carbon.

1.2 Climate change: the role of greenhouse gases

The presence of GHG in the atmosphere has shaped the life on Earth as we see it today: without them the average temperature on the Earth surface would be -15°C or -18°C (Seinfeld, 2011). However, the steep rise in anthropogenic GHG concentrations that has been ongoing since the last century has contributed to the global warming effect, which poses threats to ecosystems, species and human livelihoods (Fig. 1.3) (IPCC, 2018). The global warming observed since the mid-20th century has been driven primarily by anthropogenic emissions of three gases: CO_2, CH_4 and N_2O (Fig. 1.4) (IPCC, 2014).

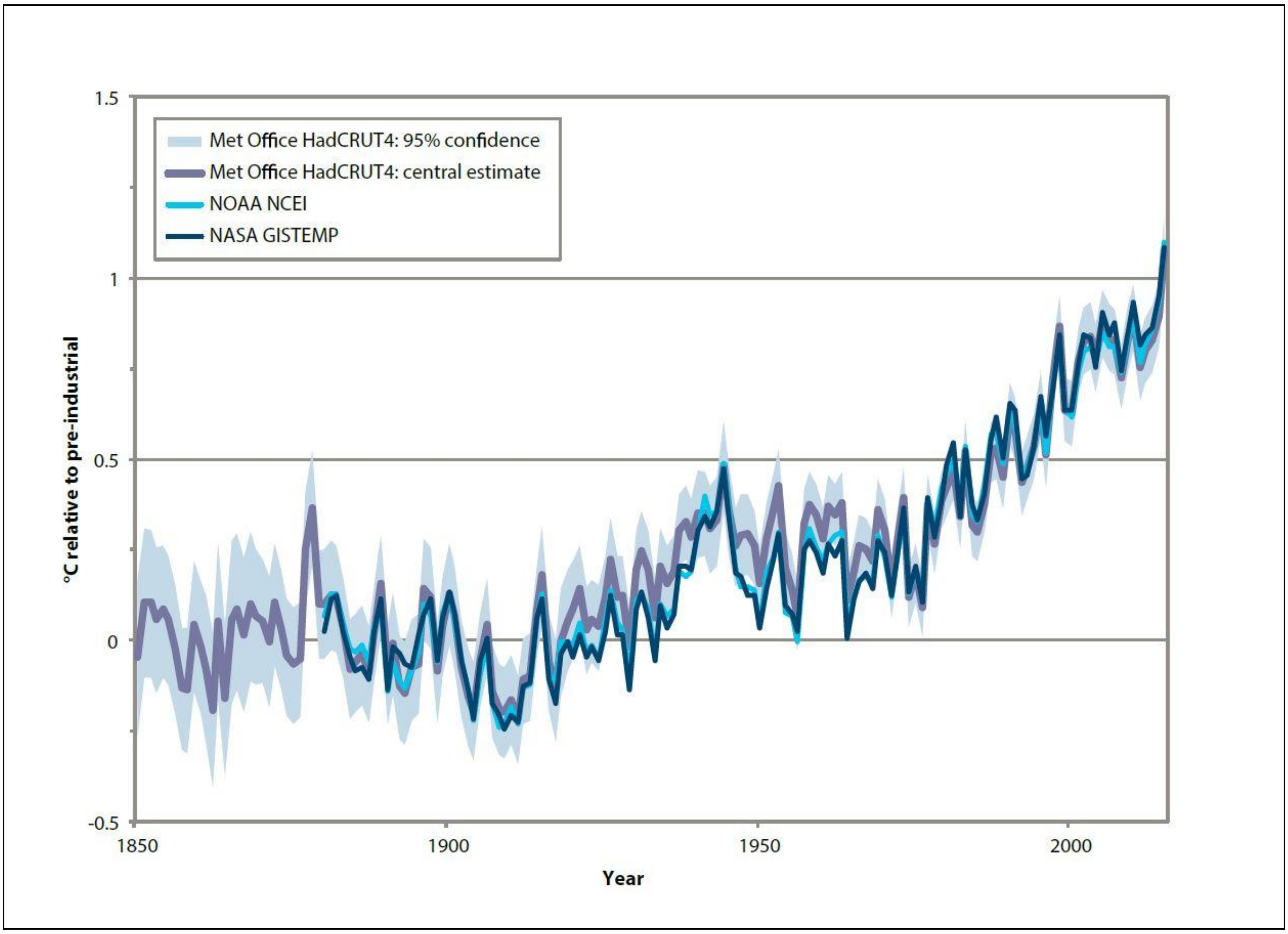


Figure 1.3: Global mean surface temperature changes as compared to the preindustrial (years 1880-1899) values.

Source: Adaptation Sub-Committee, 2016

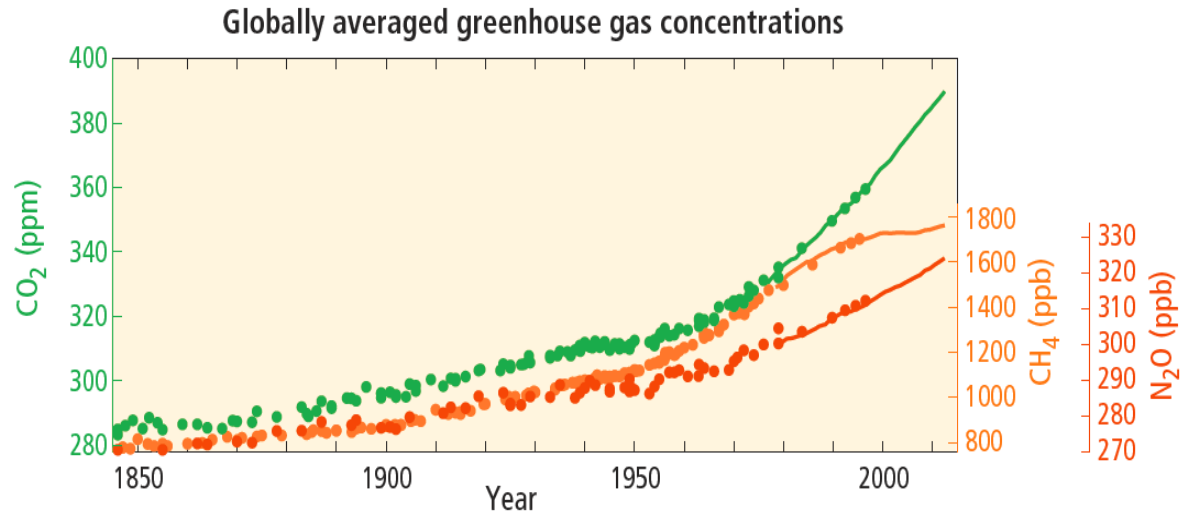


Figure 1.4: Global mean concentrations of CO_2, CH_4 and N_2O. Dots – data obtained from ice cores; lines – direct measurement.

Source: IPCC, 2014

Methane accounts for 16% of the greenhouse effect (Aydin et al., 2010) and its atmospheric concentration is increasing at a rate of 0.003 µmol mol^{-1} year^{-1} (Butenhoff and Khalil, 2007). Anthropogenic sources constitute 60% of all CH_4 emissions, to which agricultural production is the highest contributor (>50% of all anthropogenic emissions) (Karakurt et al., 2012). It is accepted within the scientific community that once a point of no return (defined as a threshold atmospheric CO_2 concentration or a threshold temperature increase) is reached, it will become impossible to reverse changes to the climate by reducing anthropogenic GHG emissions (van Zalinge et al., 2017; IPCC, 2018), although the usefulness and relevance of such a point in regards to risks to human systems is a matter of ongoing debates (Victor and Kennel, 2014; van Zalinge et al., 2017). There is a consensus that the future climate will exhibit increased mean atmospheric temperatures and higher sea levels, altered spatial and temporal patterns of precipitation and drought and more frequent occurrence of extreme weather events (IPCC, 2014). The sea level has been rising at a rate of 3 mm per year as a consequence of melting Arctic and Antarctic ice sheets and glaciers as well as thermal expansion of the oceans (Jenkins et al., 2003). Extreme weather events, such as heatwaves and increased precipitation and drought occurrence, have been becoming more frequent (IPCC, 2014; Adaptation Sub-Committee, 2016). Nevertheless, the extent and magnitude of these changes in climatic events are not certain. The degree of the predicted climate warming varies depending on the RCP (Representative Concentration Pathway) scenario (Fig. 1.5) (IPCC, 2014). The RCP number represents the predicted total radiative forcing in watts per m^2 (ex. RCP 6.0 is 6 W m^2) (IPCC, 2014).

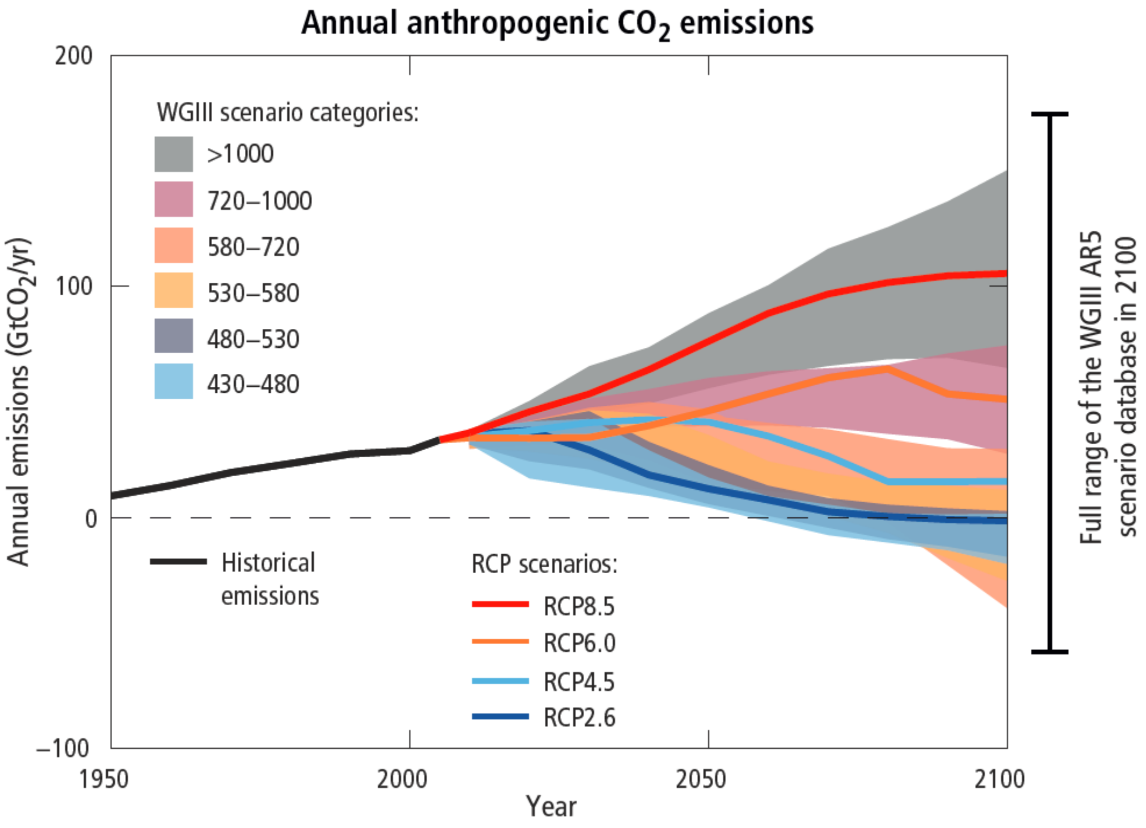


Figure 1.5: Predicted CO_2 emissions (lines) and CO_2 concentrations (fields) according to various RCP scenarios. The concentrations are in ppm. WGIII AR5 – Working Group III 5th Assessment Report.

Source: IPCC, 2014

1.3 Production of greenhouse gases in organic soils

Position of the water table plays a crucial role in determining the rate of organic matter decomposition in waterlogged soils (Rydin and Jeglum, 2006). Microbial decomposition of SOM into CO_2 occurs in aerobic conditions, whereas production of CH_4 in soil requires the presence of anaerobiosis (Luo and Zhou, 2006). Natural (undrained) peatlands are predominately CO_2 sinks and CH_4 sources, however, once drained, CO_2 emissions exceed CO_2 absorption by plants while CH_4 emissions cease or become negative (CH_4 uptake) (Kirk, 2004). Microbial decomposition of organic compounds under oxic conditions involves depolymerisation of complex structures into simple forms that can be assimilated by microorganisms (Wei et al., 2014). Microorganisms decompose organic matter by excreting enzymes (Allison, 2005; Sinsabaugh et al., 2008). Bacteria and fungi cannot assimilate most of organic compounds found in soil due to their insolubility or high molecular weight: in order to gain access to them microorganisms release extracellular enzymes (exoenzymes) that degrade complex polymers into forms which can easily pass through cell membranes (Kutsch et al., 2009; Tveit et al., 2015). There is much variety in efficiency of degradation of chemical compounds between microbial communities. Fungi can degrade all organic compounds, as opposed to most bacteria, which lack the ability to produce enzymes capable of decomposing the most recalcitrant materials, such as lignins (Cotrufo et al., 2009). Moreover, degradation of complex compounds often requires cooperation of several bacterial communities, each specialising in decomposition of a given macromolecule (Chapin et al., 2012). Additionally, the composition of microbial communities may vary with season (Andert et al., 2012). There is more complexity involved in the release of CH_4 into the atmosphere as it depends on both production of CH_4 by methanogenic bacteria (which belong to the *Archaea* group) and its consumption (oxidation) by methanotrophic microorganisms (Dedysh et al., 1998). Methane oxidation is performed mainly by *Proteobacteria* and *Verrucomicrobia* (Tveit et al., 2015). Unlike the majority of decomposing microorganisms, methanogens are exclusively anaerobic and so CH_4 can only be produced in environments devoid of oxygen (Rydin and

Jeglum, 2006; Szafranek-Nakonieczna and Stępniewska, 2015). Since methanotrophs are intolerant of anoxic conditions, oxidation can only take place in the rooting zone, where oxygen content is the highest, therefore the position of the water table directly influences the balance between the oxidation to CO_2 and the release of CH_4 in soils (Le Mer and Roger, 2001; Couwenberg, 2009). The position of the water table determines the extent of the trade-off between emissions of CO_2 and CH_4: at high water table levels anoxic conditions dominate and create a favourable environment for methanogenesis, whereas production of CO_2 is suppressed due to the oxygen requirement of decomposing microorganisms (Strack et al., 2004; Karki et al., 2016; Poyda et al., 2016). Conversely, at low water tables oxygen can more freely access SOC, which leads to CH_4 consumption by methanotrophs and increased activity of microorganisms which respire CO_2 (Couwenberg, 2009; Maljanen et al., 2010). Soil CH_4 emissions to the atmosphere occur via three pathways: diffusion in soil, ebullition (release of CH_4 bubbles) and transport through aerenchyma of certain plants (such as sedges) (Rydin and Jeglum, 2006; Sheppard et al., 2007; Serrano-Silva et al., 2014). Increases in soil temperature lead to higher rates of organic matter decomposition, which translates into rising emissions of CO_2 (Rustad et al., 2001; Ziegler et al., 2013). The effects of warming on CH_4 fluxes are not as easy to predict, since the respective activities of methanotrophs and methanogens may not be affected to the same extent (Kim et al., 2012; Van Winden et al., 2012; Pedersen et al., 2017).

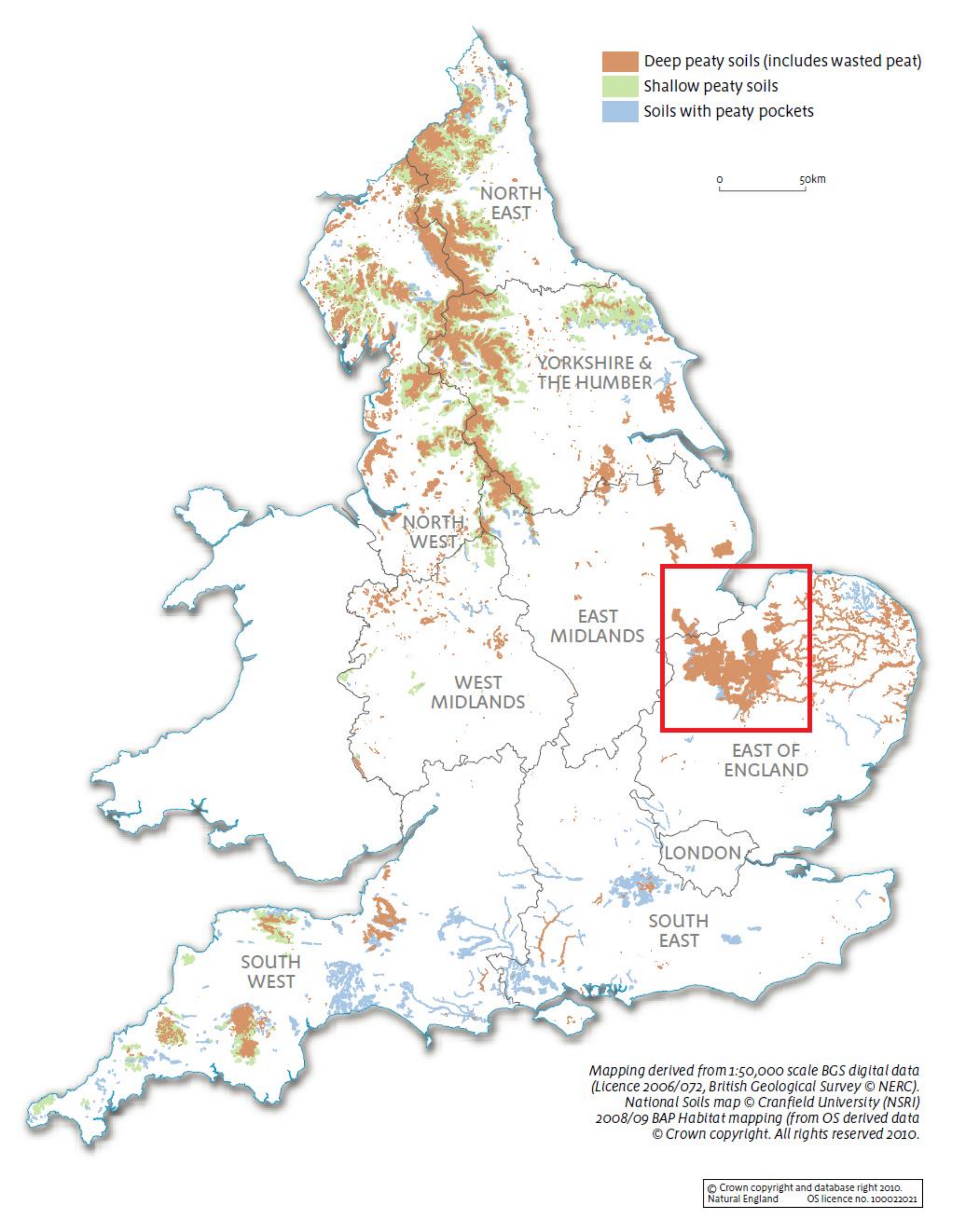
1.4 Impact of climate change on agriculture in the UK

Climate change will pose a serious risk to global food security (IPCC, 2014)), but these effects will vary regionally. In the UK, 71% (17.4 million ha) of the total land area is agriculturally-used and 4 million people are employed in the agricultural and food sector (Defra, 2019). The food produced within the UK constitutes more than a half of all food consumption in the country (Knox et al., 2010). Climate change will pose challenges as well as opportunities for UK agriculture. UK summers will be hotter and drier while winters will be wetter and milder (Adaptation Sub-Committee, 2016). The growing season is expected to last longer and the average temperatures to be higher, which will make it possible to grow crops at higher latitudes and will reduce the duration of fallow, when fields are not productive (Knox et al., 2010; Adaptation Sub-Committee, 2016). The rise in atmospheric CO_2 concentration will likely facilitate more efficient use of water, nutrients and sunlight by crops, and, consequently, improve yields (Knox et al., 2010). Nevertheless, the rising sea level will pose greater flooding risk in coastal areas and the more frequent occurrence of extreme weather events will threaten crop productivity (Adaptation Sub-Committee, 2016). The sea level rise in the UK (London latitude) is estimated to reach 0.5-2.2 m, 0.8-2.6 m and 1.4-4.3 m for the RCP 2.6, RCP 4.5 and RCP 8.5 scenarios, respectively, by 2300 (Palmer et al., 2018). Climatic warming will facilitate the emergence of new pests and heighten the risk of low yields of those crops which are susceptible to bolting at higher temperatures (such as lettuce) or which need a cool dormancy period to produce harvestable yield (such as fruit trees) (Else and Atkinson, 2010; Knox, 2010). The water balance will be affected, which, in turn, will require adjustments to field practices, such as the time of planting and the water table management (Knox et al., 2010). Plant growth under global warming will be limited by insufficient N availability in soil, however, this restriction will not apply to agricultural lands, which may, however, require higher fertiliser inputs to take full advantage of the elevated atmospheric CO_2 levels and the longer growth season (Daccache et al., 2011). Yields of wheat in the UK are predicted to increase by 15-23% by 2050 due to the CO_2 fertilisation effect (Richter and Semenov, 2005). Yields of UK sugar beet are likely to rise and the increase will be higher on loams than on sands, highlighting the difficulty in estimating performance (and also CO_2 uptake) of each crop depending on the soil type it is farmed on (Richter et al., 2006). Likewise, adjustments of management practices will play an important role in maximising yields in the future climate: for instance, UK potato yields are predicted to increase by 3-6% by 2050 under unchanged fertiliser application regimes, but the rise should be higher (13-16%) if irrigation and fertiliser needs are adequately met (Daccache et al., 2011). The rise in global mean temperature will likely accelerate decomposition of organic soils, increasing emissions of GHG to the atmosphere (Waddington et al., 1998; Updegraff et al., 2001; Tarnocai, 2009), however, the effects of the climate change on the total C balance of agricultural ecosystems might be not be easy to predict due to difficulties in estimating the reaction of specific crops to higher temperatures and CO_2 fertilisation (Shaw et al., 2014; Carter et al., 2016; Osanai et al., 2017).

1.5 The East Anglian Fenlands

The East Anglian Fenlands (the Fens) are a low-lying area covering south-west Norfolk, north-west Suffolk and north-central Cambridgeshire (Fig. 1.6) (Seale, 1975). A large portion of the Fens is situated below the sea level, which necessitates drainage of agriculturally-used lands. This is done with a system of pumps, ditches and dykes which are connected to rivers (Seale, 1975). Major draining works occurred in the 17th century onwards, and the pace of drainage accelerated in the early 20th century with the introduction of diesel and electric water pumps (Seale, 1975). The climate of the East of England is characterised by low (as compared to the UK mean) rainfall and a higher diurnal and seasonal temperature amplitude, with cold winters and hot summers (Hodge et al., 1984). The annual rainfall is less than 600 mm per year, making it one of the driest parts of the country (Hodge et al., 1984). The average rainfall does not vary much between months (Seale, 1975). The Fens are a major contributor to UK's food supply: more than one-third of vegetable production and one-quarter of potato production in England come from the area (Natural England, 2015). The area of the Fens is covered by loamy and clayey soils of coastal flats with naturally high groundwater (51%), loamy and sandy soils with naturally high groundwater and a peaty surface (28%), fen peat soils (7%) and others (9%), which include lime-rich soils (Natural England, 2015). Soils of the Fens are characterised by high fertility: around 90%

of the land is classifies as Grade 1 or Grade 2 (the highest fertility values) (Natural England, 2015). In recent years farmlands of the Fens witnessed a shift towards horticulture and cultivation of stockfeed and oil seeds at the expense of cereal cropping, although cereals still cover the largest farming area (137 000 ha in 2009) (Natural England, 2015). The agricultural lands of the Fens face pressure from intensive farming, with peats being especially vulnerable to degradation through erosion, shrinkage and organic matter oxidation (Fig. 1.6) (Seale, 1975; Holman and Kechavarzi, 2011).



Mapping derived from 1:50,000 scale BGS digital data (Licence 2006/072, British Geological Survey © NERC). National Soils map © Cranfield University (NSRI) 2008/09 BAP Habitat mapping (from OS derived data © Crown copyright. All rights reserved 2010.

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Figure 1.6: Peatland coverage in England. The Fens are in the red rectangle. Deep peaty soils: areas covered with a majority of peat >40 cm deep; shallow peaty soils: areas with a majority of soils with peat 10–40 cm deep; soils with peaty pockets: areas of mostly non-peat soils, supporting smaller pockets of deep peat. Source: Natural England, 2010

In total, the peats of the Fens cover 31 517 ha and are primarily used for intensive agriculture (Fig. 1.7). Holman and Kechavarzi (2011) estimated that the peat soils of the Fens waste at a rate of 0.5 Tg C year^{-1}, with higher wastage rates in areas with a low water table and which undergo liming and frequent wetting and drying cycles. Two-thirds of the Fens peat may be lost by 2050 as a result of oxidative degradation (Burton and Hodgson, 1987). The rate of peat loss will likely accelerate in the warmer climate (Gill et al., 2017; Bader et al., 2018; Duval and Radu, 2018), however, adopting conservation practices relating to water table management may preserve the fertile soils of the Fens for longer (Kechavarzi et al., 2007; Musarika et al., 2017).

a)

Peat class	Estimated area (ha)
Thick peat*	9251
Thin peat	14164
Peat at depth	8102
Total	31517

b)

	Land cover		
Peat thickness	Intensive arable (drained and cultivated)	Intensive grassland (drained)	Semi-natural (largely undrained)
Thick (> 1 m)*	2.1	0.8	0.4
Thin (< 1 m)	1.3	0.7	0.1

Figure 1.7: a) The area covered by peat soil within the Fens. b) Fenland peat wastage rates (cm yr^{-1}) depending on the land use type. Thick peat: >1 m depth; thin peat: <1 m depth. * Referred to as 'Deep peat' in Holman (2009).

Source: Holman, 2011

1.6 Aims of the presented research

Given the rapid climatic changes which pose risk to agricultural ecosystems, in here I present the outcomes of three experiments aimed at enhancing our understanding of the C cycle in agriculturally-utilised peat soils of the Fens and advising farmers on sustainable practices. The experiments evaluate the effects of climate change and water table management on performance of three crops: radish (*Raphanus raphanistrum* subsp. *sativus* (L.) Domin), celery (*Apium graveolens* var. *dulce*) and romaine lettuce (*Lactuca sativa* (L.) var. *longifolia*) grown on intact cores of fen peat to preserve the physiochemical properties of the substrate, and using commercial fertilizer applications. These crops were chosen because of their commercial profitability and assumed heightened tolerance to waterlogging.

The major questions I endeavour to answer in this work are:

1. Is it possible to reconcile peat preservation via water table manipulation with agricultural productivity? Can similar or higher yields be obtained at a higher water table level?
2. How will water table manipulation affect C budget of agricultural peats? Can raising the water table reduce peat C loss as CO_2, CH_4 and DOC?
3. How will the climate change affect crop yield? Will rising temperatures and CO_2 concentrations improve or limit horticultural productivity of the peat soils of the Fens?
4. How will the global warming affect agricultural peat loss and C cycling?

The research aims of each experiment are as follows:

Experiment 1: I explore the effects of water table manipulation (two water table levels: -30 cm and -50 cm) and atmospheric CO_2 enrichment (two CO_2 levels: ambient and 850 ppm) on the yield of radish, radish nutrition, soil respiration (Rh), Net Ecosystem Exchange (NEE), Gross Primary Production (GPP) and CH_4 emissions. I hypothesise that raising the water table from the field level of -50 cm to -30 cm would not have negative implications for the radish bulb yield whereas increasing the atmospheric CO_2 level to 850 ppm would increase the total biomass of radish.

Experiment 2: I explore the impacts of raising the water table (two water table levels: -30 cm and -50 cm), fertilization (two fertilisation levels: fertilised and not fertilised) and warming (two temperature levels: ambient and ambient +5°C) on the yield of celery, Rh, NEE, GPP and emissions of CH_4, as well as C leaching out of the system as DOC. I hypothesise that raising the water table from the depth of -50 cm to -30 cm would not affect the celery yield, however, it would decrease Rh, while only slightly increasing CH_4 emissions, and it would increase DOC concentration in drainage water. I expect the 5°C warming to increase the celery yield, Rh and DOC content in drainage water. I hypothesize that fertiliser input would increase celery yield, GHG emissions and drainage water DOC concentration.

Experiment 3: I test the impact of raising the water table (three water table levels: -30 cm, -40 cm and -50 cm) and warming (two temperature levels: ambient and ambient +2°C) on production of romaine lettuce leaves and roots and GHG fluxes. I hypothesise that raising the water table would decrease Rh and increase NEE, GPP and CH_4 emissions, and a water table of -40 cm would not negatively affect leaf biomass of romaine lettuce. I also hypothesise that the 2°C warming would lead to higher Rh and enhance production of romaine lettuce leaves. In this experiment all peat cores are fertilised to better imitate the field conditions.

These experiments, for the first time, allow for evaluation of performance of different commercially important crops under various water table depths, temperature conditions and atmospheric CO_2 concentrations. The knowledge gained in the course of this research is important for assisting farmers and policy makers in making decisions on land management that concern food production and GHG emissions.

Chapter 2

Emissions of CH_4 and CO_2 and radish yield under two water table levels and CO_2 enrichment

2.1 Introduction

Peatlands used in agricultural production require drainage, which causes rapid peat wastage and massive release of CO_2 to the atmosphere (Global Environmental Centre, 2008; Dixon et al., 2014; Carlson et al., 2016). Raising the water table has the potential to slow down decomposition of peat and extend the lifespan of fertile lowland peats of the UK, such as the Fens: an area of intensive agricultural production in the East of England (Kechavarzi et al., 2007; Taft et al., 2018; Peacock et al., 2019). Raising the water table is a proven means of reducing soil CO_2 emissions (van den Akker et al., 2010; Schrier-Uijl et al., 2014; Knox et al., 2015), however, it also runs the risk of promoting CH_4 release to the atmosphere and negatively impacting crop yield (Drew and Lynch, 1980; Maljanen et al., 2007; Schott et al., 2017). In undrained bogs water table increases reduce the size of the aeration zone, which limits the potential for CH_4 oxidation (Regina et al., 2015; Poyda et al., 2016; Kandel et al., 2018). Consequently, undrained peat sites are globally important sources of CH_4, which has 28 times higher GWP (global warming potential) per molecule than CO_2 over a 100 year period (IPCC, 2014). However, in agriculturally-utilised peats, contrary to the expectations from the studies of undrained, uncultivated peatlands, high water table levels have not been found to promote CH_4 emissions. Taft et al. (2018) showed that CH_4 fluxes were around zero both when the water table was at the surface level and when it was at a depth of -15 cm. There was no difference in CH_4 flux (which was close to zero) from agricultural peat when the water table rose seasonally from below -60 cm to -40 cm and -30 (Kandel et al., 2018) and no difference in CH_4 emissions between water table levels of -15 cm, -35 cm and -55 cm (Susilawati et al., 2016). Annual CH_4 emissions were similar between peat sites with mean annual water table levels of -55 cm, -45 cm and -25 cm, moreover, CH_4 fluxes were lower in winter, when the water table level was higher, indicating that CH_4 production was not dependent on changes in hydrological conditions (Schrier-Uijl et al., 2014), but might be more sensitive to temperature.

Given the importance of the Fens cultivation for food security in the UK (NFU, 2019), the rates at which they are being wasted by oxidation, shrinkage and wind-erosion, and their disproportionately large contribution to GHG emissions from agriculture (Natural England, 2010), there is an urgent need to address these issues. One method of preservation of the agricultural areas of the Fens would be raising the water table during winter, when fields are not utilised or have low productivity due to low temperatures and low irradiance. Increasing the water table to the surface level off-season on farmed peat was found to considerably reduce CO_2 release and not affect CH_4 emissions during and after flooding as the post-drainage GHG emission pulse was negligible (Taft et al., 2018). However, it is not clear to what extent post-drainage conditions would affect crops grown in the early spring of the UK climate, when low temperatures limit evaporation, possibly contributing to waterlogging. Many crops are highly sensitive to waterlogging due to the presence of ions and chemical compounds under low redox conditions that may be toxic to plants (Lynch, 1978; Kirk, 2004; Dowrick et al., 2006; Loeb et al., 2008) and there is much uncertainty as to how long these by-products may linger in peat following drainage (Knorr et al., 2009; Estop- Aragonés et al., 2013). Moreover, leaching of nutrients may occur when the water table level is high (Damman, 1978), which would need to be addressed by increased application of fertilisers. It is therefore crucial to determine whether peat conservation efforts using seasonal water table manipulation can be reconciled with proper growth of crops.

Radish (*Raphanus raphanistrum* subsp. *sativus* (L.) Domin) is one of a number of high value salad crops that are commonly grown in the UK on lowland peatland soils. Such soils are very effective at holding water (Hallema et al., 2015), and water supply to the crop is often precisely controlled by maintaining the depth of the water table that ensure good growth. One of the most important regions for field-grown salad crops like radish are the East Anglian Fenlands (The Fens), which provide 37% of vegetable production in the UK and sustain around 4000 farms (NFU, 2019). The peat from the Fens is undergoing rapid oxidative degradation due to drainage and cultivation required to grow crops, with peat wastage rates being around 2.1 cm yr^{-1} for thick (>1 m) peat and 1.3 cm yr^{-1} for thin (<1 m) peat (Holman and Kechavarzi, 2011). This suggests that the peat of the area will be lost within 100 years if the current management practices are kept. Since much of the Fens area is at or slightly below the sea level, maintaining the water table depth below the peat surface requires pumping of water into a system of ditches and canals (Darby, 1956). As peat shrinks, the volume of water that needs to be pumped out rises, increasing the cost and energy use (Natural England, 2015). Furthermore, the sea level rise due to thermal expansion of the oceans and melting of land-based ice with global warming further compounds these issues (IPCC, 2014; Palmer et al., 2018).

Atmospheric CO_2 concentrations are predicted to rise due to heightened anthropogenic emissions to 580-1000 ppm CO_2 by 2100 according to the RCP 4.5 and the RCP 6.0 scenarios (IPCC, 2014). Much attention is being paid to how plants, including crops, will react to rising atmospheric CO_2 levels. There is a large body of literature which reports decreases in stomatal conductance in plants subjected to elevated CO_2 conditions (Curtis et al., 1996; Houshmandfar et al., 2015; Osanai et al., 2017; Urban et al., 2017). However, these reductions in stomatal conductance are not associated with decreased ability to photosynthesise, on the contrary, a number of studies demonstrate that increasing atmospheric CO_2 could potentially lead to greater photosynthetic assimilation of CO_2 and higher growth rates (Tognoni et al., 1967; Kriedemann et al., 1976; Daymond et al., 1997; Fernández et al., 2002; Ainsworth and Rogers, 2007; Osanai et al., 2017; Uddin et al., 2018). This so-called 'fertiliser effect' occurs as the current atmospheric levels of CO_2 (~410 ppm) are still suboptimal for photosynthetic activity of most plants (Tognoni et al., 1967; Hay and Porter, 2006). Atmospheric enrichment with CO_2 can lead to better water use efficiency (WUE) through a higher photosynthetic rate (Pazzagli et al., 2016) and effects on stomata, such as enhanced stomatal closure and lower stomatal density (Christy et al., 2018; Liu et al., 2018; Kumar et al., 2019). Additionally, leaf concentration of the photosynthetic enzyme Rubisco (a N-based enzyme essential in C assimilation), and hence N, may decrease in plants fertilised with CO_2 as photosynthesis becomes more efficient: growth of plants is not negatively affected under such circumstances (Uddling et al., 2018; Du et al., 2019). The Leaf Area Index (LAI; area of leaves per unit area of ground) may also increase at elevated CO_2 values, which would improve radiation use efficiency (RUE) (Daymond et al., 1997): this would be expected to translate into higher biomass production. Photosynthetic downregulation (negative acclimation) is a process where an increase in photosynthetic activity in reaction to higher atmospheric CO_2 level or light intensity is later reversed (Aranjuelo et al., 2005; van Gestel et al., 2005). The process is often attributed to metabolic changes in cells, such as increasing N limitation (Wolfe et al., 1998; Stitt and Krapp, 1999). Studies sometimes report photosynthetic downregulation in CO_2 fertilisation experiments: the photosynthetic rate can sometimes be reduced in plants exposed to elevated levels of atmospheric CO_2 for prolonged periods of time (Wolfe et al., 1998; Taub and Wang, 2008).

The physiological responses to increasing atmospheric CO_2 concentrations are of particular importance for food crops, which, as a result of fertilizer use, are often growth-limited by water supply or suboptimal atmospheric CO_2 values. Vegetables with harvestable bulbs and roots have high water requirements and were shown to produce higher yields (of onion bulbs, carrot roots and beetroot roots) under CO_2 enrichment of 450-750 ppm (Wurr et al., 1998). Raising atmospheric CO_2 concentration to ~500 ppm increased onion bulb yield by 29-51 % (Daymond et al., 1997). Similarly, Idso and Kimball (1988) found that atmospheric CO_2 at 640 ppm increased biomass storage in roots of radish and raised its root:shoot ratio by 36%. Radish yields also increased when the atmospheric CO_2 concentration was raised to 750 ppm in a more recent study (Usuda, 2004). In a study on the Fens peat Musarika et al. (2017) found that dry bulb biomass of radish was unaffected by increasing CO_2 concentration to 800 ppm, while it had a positive effect on dry leaf biomass.

Although a number of studies reported that increasing the water table level could slow decomposition of peat (Regina et al., 2015; Poyda et al., 2016; Taft et al., 2018), the effects of water table manipulation on crop productivity have not been extensively researched (Dodds et al., 1997; Stanley and Harbaugh, 2002; Musarika et al., 2017; Matysek et al., 2019). Consequently, it becomes difficult to advise farmers on hydrological management which would minimise peat loss while maintaining a similar level of horticultural output. Renger et al. (2002) reported that a water table of -30 cm reduced peat decomposition by 30-40% while retaining 90% of grassland yield: as a result field lifespan could be extended. Tomato yield was found to be the highest at a -60 cm water table and the lowest when the water table was -1 m (the range of applied water table depths was between -30 cm and -1 m) (Dodds et al., 1997). Tuber yield of *Caladium* grown on peat was better when the plant was grown at a water table of between -30 cm and -45 cm than at a deeper water table of -60 cm (Stanley and Harbaugh, 2002). Performance of radish on peat under an increased water table level and a higher atmospheric CO_2 concentration was examined by Musarika et al. (2017), however, the primary focus of their study was peat oxidation and GHG emissions, with the growth response of radish being a more minor part of the work. They showed that raising the water table from the field level of -50 cm to -30 cm increased radish bulb dry biomass. Nevertheless, the paper they published has a major drawback of not reporting the significance of the treatment effects on fresh biomass as a whole or fresh weight of specific plant organs, such as bulbs: the critical variable for farmers. The total fresh biomass weight they reported appears to show an interaction effect between the water table and the CO_2 level, whereby the biomass increase with raising the water table to -30 cm is only seen in the ambient, and not at the elevated (800 ppm), CO_2 treatment. This is not elaborated upon in the discussion and, surprisingly, the statistical analysis on the total radish biomass does not report any interaction effect between the water table and the CO_2 treatments. Therefore, their study leaves some questions unanswered and is not sufficiently clear and unambiguous to be used to advise farmers on the viability of raising the water table position.

In this study, I attempted to evaluate the outcomes of a simulated off-season flooding followed by an increase in the water table level from -50 cm (field level) to -30 cm, and an atmospheric

CO_2 increase from the ambient level (~410 ppm) to 850 ppm on yield of radish and emissions of CO_2 and CH_4 from the Fenland peat. Radish was chosen due to its fast growth, its economic importance in the horticulture of the Fens and its high water content, which would presumably allow it to take full advantage of conditions of high water availability. The two CO_2 levels represent the current ambient atmospheric CO_2 concentration (aCO_2) and the doubled value of this concentration (eCO_2), which is predicted to be reached by 2100 according to the RCP 6.0 scenario (IPCC, 2013). The depth of -50 cm is the water table currently used on the field. The water table of -30 cm is proposed as a level at which GHG emissions fall considerably while productivity (of grassland) is retained (Renger et al., 2002). The -30 cm water table also reflects the findings of Stanley and Harbaugh (2002), and Murisaka et al. (2017) who showed that raising the water table to similar depths did not considerably affect crop yield. It is also the optimal water table level at which CH_4 flux is negative (uptake) and emissions of CO_2 are low (Regina et al., 2015). I subjected peat to flooding before conducting the experiment to imitate post-flooding conditions of English early spring. The set-up I implemented in this experiment is similar to Musarika et al. (2017): I used the same water table and CO_2 treatment levels. However, what differentiates this study from the one by Musarika et al. (2017) is the exposition of peat to simulated winter flooding prior to planting of radish and commencement of GHG measurements, and full reporting of radish biomass, including fresh weight of the edible portion of the crop (the bulb). In addition, I investigated the effects of the water table and CO_2 treatments on available N pools in peat in order to better understand how the water table and the atmospheric CO_2 concentration may affect soil nutrient availability. A detailed elemental analysis of the radish leaves was performed to uncover the legacy of the applied treatments on plant mineral nutrition (Ca, Cl, Fe, Mg, Mn, P, S, Fe and Zn) and possible exposure to potentially toxic concentrations of elements (e.g. Al, Cd, Pb, Zn) that may be mobilized by winter-flooding of peat. These elements could affect growth of the crop and its suitability for human consumption, although my focus was on plant nutrition affecting foliar health, so the bulbs were not analysed. In this experiment the peat was not fertilised in order to closely follow the experimental design of Musarika et al. (2017).

I hypothesised that increasing the atmospheric CO_2 concentration from the ambient concentration to 850 ppm would improve radish bulb yield. Additionally, I hypothesised that raising the water table level from -50 cm to -30 cm would have a positive impact on radish bulb biomass and would decrease the rate of peat decomposition by lowering emissions of CO_2 and keeping the release of CH_4 constant. I anticipated no changes in content of essential elements (Ca, Cl, Mg, Mn, N, P, S, Fe and Zn) in radish leaves between the two water table levels, but a lower N content in the leaves of plants grown in the eCO_2 conditions as compared with the aCO_2 treatment.

2.2 Methodology

2.2.1 Field site

The peat cores were collected from a field on Rosedene Farm in Methwold Hythe, Norfolk in autumn 2015 (Fig. 2.1). Rosedene Farm is situated on deep peat in the East Anglian Fenlands and has a yearly rainfall of below 600 mm (Evans et al., 2016) and a mean annual temperature of 10°C (Cumming, 2018). The sampling site is described in more detail in Matysek et al. (2019).

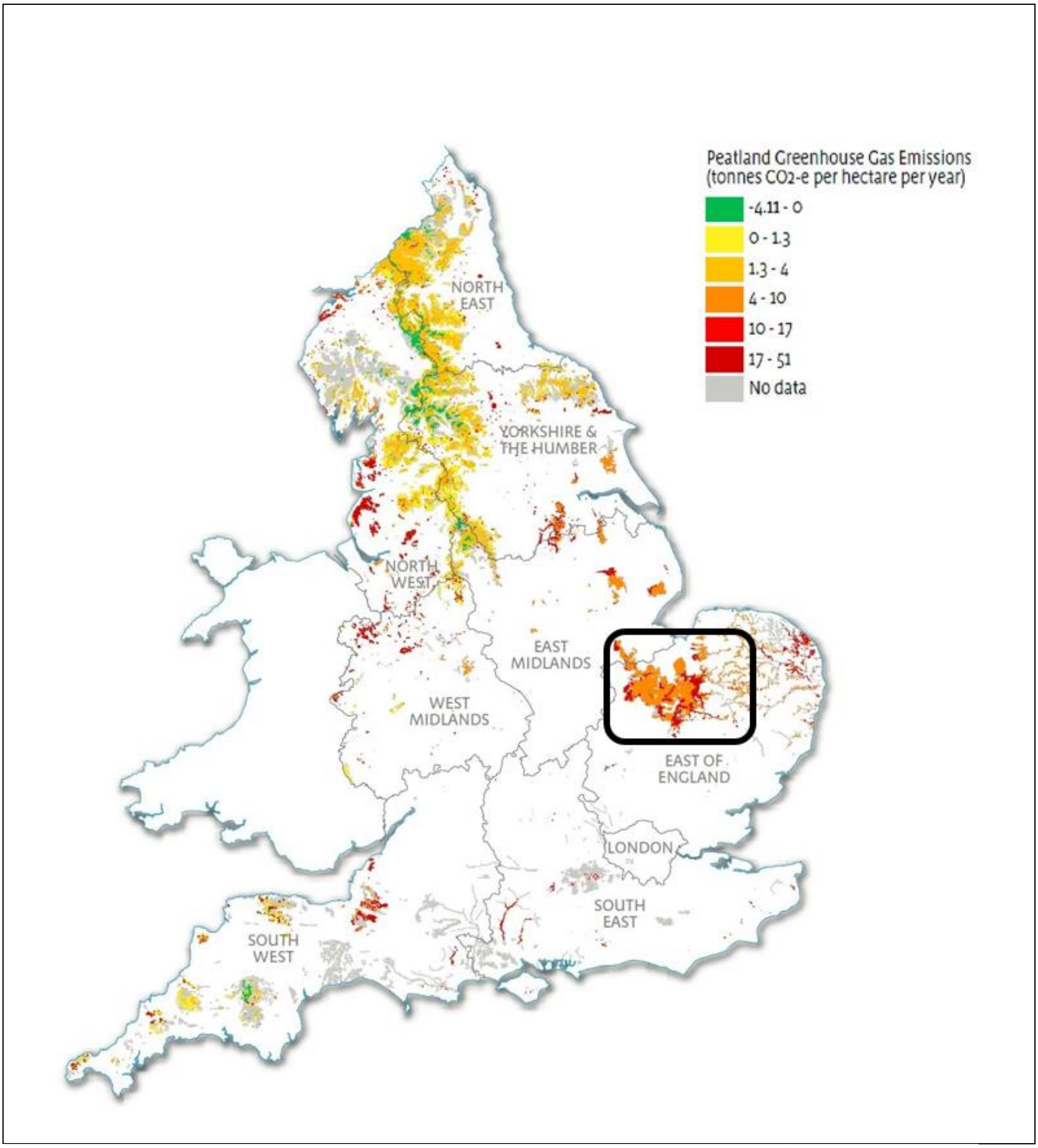


Figure 2.1: GHG emissions from English peats. The East Anglian Fenlands are in the black rectangle.

Source: Natural England, 2010

2.2.2 Sampling and core re-use

A total of 46 soil cores were collected to a depth of 60 cm and with a diameter of 11 cm, and used in the radish experiment of Musarika et al. (2017). The collection was performed using PVC pipes, which were inserted into the soil. The PVC pipes were excavated from the ground, preserving the existing soil structure within the pipes. Pipe plugs were then inserted at the bottom to retain the field soil moisture. To simulate the off-season water table increase, after the first radish crop was grown and harvested (Musarika et al., 2017), the cores were preserved by flooding and stored at a temperature of 4°C for two months, until February 2016, when they were drained to the experimental water table levels and data collection started. The same treatments were used in my experiment as in Musarika et al. (2017): crop presence and absence, two water table levels (-30 cm and -50 cm) and two CO_2 concentrations (ambient 410 ppm and elevated 850 ppm) (Fig. 2.2).

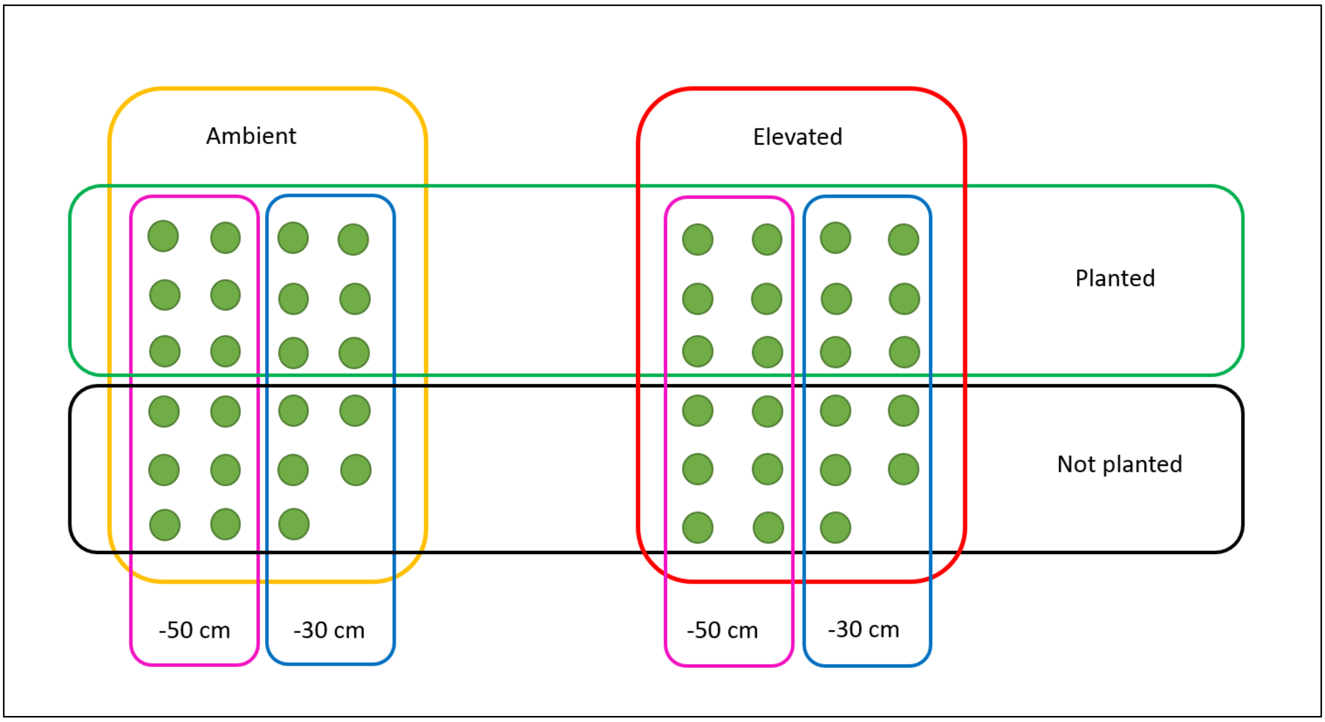
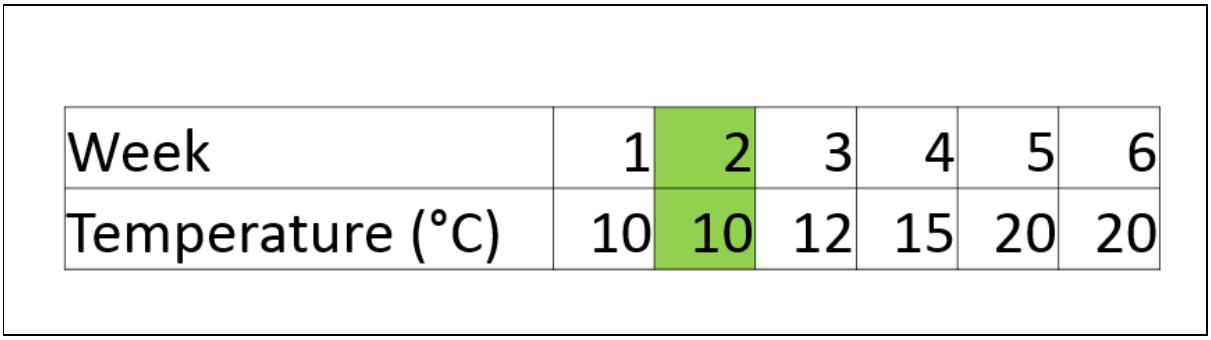


Figure 2.2: Research design. Two water table treatments: -50 cm (n=22) and -30 cm (n=24) , two CO_2 treatments: ambient (~410 ppm) (n=23) and elevated (850 ppm) (n=23), planting (n=24) and lack of planting (n=22). The total number of cores is 46.

The cores were placed in two CONVIRON BDW 40 growth chambers (Controlled Environments Ltd., Winnipeg, Manitoba, Canada) at the Sir David Read Controlled Environment Facility, University of Sheffield. The chambers regulated air temperature in real time with an accuracy of ±0.5°C. The temperature in both chambers was set to represent progressive spring warming in the East of England. The temperature settings and their changes are presented in Fig. 2.3. Day and night temperatures were set to be the same, unlike in the field, where diurnal temperature variations occur. Photosynthetically active radiation (PAR) was measured every week in both chambers. Relative humidity inside the chambers was maintained at 70%, which is similar to the relative humidity observed in the field (i.e. 70-80% from March to May, Cumming, 2018). In both chambers the daylight conditions lasted 12 h (12 h for night conditions) throughout the growth period.



Week	1	2	3	4	5	6
Temperature (°C)	10	10	12	15	20	20

Figure 2.3: Weekly temperature settings.

Radish was planted in a half of the cores (to measure NEE, GPP and ER), the other half being left uncropped in order to measure Rh. The water table in each peat core was monitored every 2-3 days with the use of 20 mm diameter drainage pipes which were inserted into the cores. These pipes had holes every 1 cm, which were protected by fine mesh to prevent their clogging with soil. Distilled water was added via the drainage pipe if necessary to maintain the required water table level; water was drained if it exceeded the set level (-30 cm or -50 cm). Soil water content was measured in the top 12 cm every week with a Campbell Scientific soil moisture probe (model CS655, Campbell Scientific, Logan, Utah, USA). Likewise, soil temperature at a depth of -10 cm was measured every week with a thermocouple connected to a datalogger (CR1000, Campbell Scientific Logan, USA). The experiment lasted six weeks. In the second week two to three radish seeds were planted in a core and the crop was harvested in week 6. Two to three plants grew in each core.

2.2.3 Measurement of GHG fluxes

Measurements of the CO_2 and CH_4 fluxes were taken once a week for six weeks using an LGR Ultra Portable Gas Analyser GGA-30p (Los Gatos Research, Mountain View, CA, USA). Two custom-made PVC chambers, both with a volume of 2.8 l, were used to record the fluxes: one transparent to record Rh in the uncropped cores and NEE in the planted cores (light measurements), and one opaque chamber to record ER in the planted cores (dark measurements). Gross Primary Production was calculated as GPP=ER-NEE. The CO_2 and CH_4 fluxes were calculated from changing concentrations in the chambers over a period of two minutes; the formula used is described in McEwing et al. (2015).

2.2.4 Harvest

After five weeks of growth radish was harvested and its bulbs and roots were cleaned under running water. The leaves, bulbs and roots were weighed (fresh biomass). The bulb, root and leaf biomass was dried at 80°C for 24 hours and weighed again (dry biomass).

2.2.5 Peat and leaf C/N ratio, peat NO_3^- and NH_4^+ content

Soil samples were taken at harvest from two depths: 0-5 cm (topsoil) and 30-35 cm (deep soil). The soil and leaf samples for the C/N analysis were dried at 105°C, ground to fine powder in a ball mill (Fritsch Pulverisette, Germany) and analysed on a Vario EL Cube Elementar C/N analyser. Soil samples were taken from planted cores in order measure concentrations of NO_3^- and NH_4^+. The samples were taken from two depths: 0-5 cm (topsoil) and 30-35 cm (deep soil). The samples were dried at 40°C and 1 g or 2 g of soil was extracted in 1 M KCl (in 10 ml or 20 ml, respectively) (Allen, 1989). Drying soil material at 40°C is an accepted procedure for analysing soil for NO_3^- and NH_4^+ content as their losses are minimised (Allen, 1989). The extracts were analysed using the colorimetric method (Mackereth et al., 1989; Mulvaney, R.L., 1996) on a 7315 UV/Vis spectrophotometer.

2.2.6 Elemental analysis of radish leaves

Radish leaves were dried at 105°C and ground to fine powder in a ball mill (Fritsch Pulverisette, Germany). The dried material was digested in acids following the protocol attached in Annexe 2 and analysed by ICP-MS (Thermo-Fisher Scientific iCAP-Q; Thermo Fisher Scientific, Bremen, Germany). The results were processed using the Qtegra software (Thermo-Fisher Scientific). The elements analysed were: Al, Ca, Cd, Cu, Fe, K, Mg, Mn, P, Pb, S, Zn. Chlorine (Cl) content was analysed using X-Ray Fluorescence on an Olympus XRF analyser.

2.2.7 Data analysis

The statistical analysis was performed using the open source programme R version 3.5.3 (R Development Core Team, 2019). Total weight of each yield component (roots, bulbs, leaves) was divided by the number of plants in a core. Linear models were used to analyse the influence of the water table and CO_2 treatments, soil water content, soil N content on biomass weight, the ratio of aboveground to belowground biomass (AB/BG ratio), leaf mineral content, peat NO_3^- and NH_4^+ concentrations.

Since a number of cores contained two, instead of three, radish plants, five cores were removed from the GHG analyses: two from the eCO_2 -30 cm treatment, two from the aCO_2 -30 cm treatment and one from the aCO_2 -50 cm treatment. The effects of plants on the GHG fluxes would otherwise not be comparable across all replicates. To analyse the GHG and environmental conditions data I used both linear models and linear mixed models. The linear models were executed using the 'lm' function in R. The linear mixed effects models were used to test the effects of water table, CO_2 concentration, soil water content, planting and soil temperature on emissions of CO_2 and CH_4 and soil water content for the entire dataset with 'week' and 'core' as random effects (to take into account the temporal and spatial pseudoreplication). The CH_4 flux in the linear mixed model analysis of the effects of planting and water table level was log-transformed to meet the assumptions of linear models. The CH_4 flux was not transformed in other instances. The linear models were used on soil water content and CO_2 and CH_4 fluxes averaged over the entire experiment. For the linear mixed models analyses I used the lme4 package (Bates, Maechler and Bolker, 2014) and reported $\chi 2$ in the place of the F-value. A t-test was used to determine whether any significant difference in PAR was present between the two growth chambers.

The adequacy of all models was assessed by visual inspection of residual plots. When the mixed effects models were used, the statistical significance of each factor was determined by likelihood ratio tests performed with the Anova () function between the full model and a model that only included the random effects (weeks and cores). The statistical significance levels used were P-value <0.05 and >0.01 (*), P-value < 0.01 and > 0.001 (**), and P-value <0.001 (***).

2.3 Results

2.3.1 Growth conditions

PAR was significantly (t=2.97, df=9.79, P= 0.014) higher (755 µmol) in the eCO_2 chamber when compared to the aCO_2 chamber (722 µmol), but the difference was less than 5%. Soil water content in the top 12 cm did not vary between the two chambers in the unplanted cores, however, in the cropped cores it was significantly higher in the eCO_2 chamber (by 6%). Soil water content in the top 12 cm was significantly higher in the -30 cm treatment: in planted cores by 20%, in unplanted cores by 12% (Table 2.1, Fig. 2.4).

	lmer			lm		
Soil water content (planted)	**df**	**χ2**	**P-value**	**df**	**F-value**	**P-value**
Water table	1	25.24	**<0.001 *****	1, 20	22.19	**<0.001 *****
CO_2 level	1	4.11	**0.043 ***	1, 20	7.7	**0.012 ***
Soil water content (not planted)						
Water table	1	13.49	**<0.001 *****	1, 19	20.31	**<0.001 *****
CO_2 level	1	0.1	0.749	1, 19	2.48	0.132

Table 2.1: Effects of water table level (-30 cm or -50 cm) and CO_2 concentration (ambient or elevated) on soil water content in planted and unplanted cores. 'Lmer' denotes the linear mixed model (which included 'week' and 'core' as random effects) and 'lm' the linear model (which was applied to values averaged over the entire experiment). Water table and CO_2 concentration are categorical variables. In lmer n=276 (planted cores) and n=180 (in unplanted cores). * - may be significant; ** - significant; *** - highly significant; df – degrees of freedom.

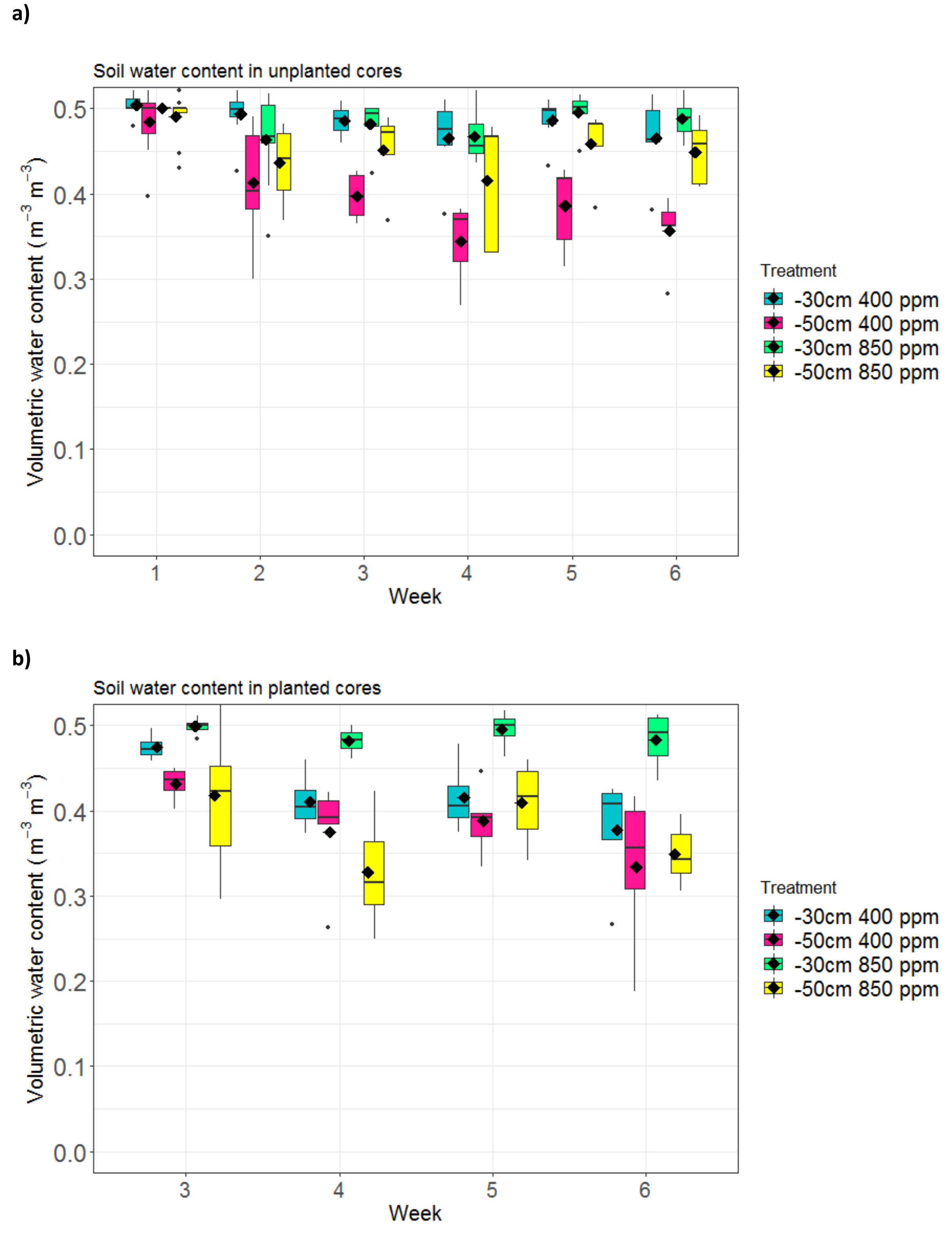


Figure 2.4: Average weekly soil water content in unplanted (a) and planted (b) cores.

2.3.2 Plant biomass

The fresh and dry bulb, root and leaf weights were negatively affected by the higher water table (Table 2.2, Fig. 2.5). The fresh and dry bulb weights were significantly lower in the -30 cm water table by 59% ($P<0.001$) and 41% ($P<0.001$), respectively. The -30 cm water table level significantly reduced the fresh and dry root biomass by 34% ($P<0.022$) and 37% ($P<0.005$), respectively, and significantly decreased the fresh and dry leaf biomass by 64% ($P<0.001$) and 49% ($P<0.001$). The eCO_2 treatment significantly decreased the fresh bulb (by 37%), fresh leaf (by 40%) and dry bulb biomass (by 34%). The fresh root, dry root and dry leaf weight were not affected by the CO_2 treatment. The total fresh and dry biomass weight was significantly lower in the -30 cm water table by 60% and 45%, respectively. The eCO_2 treatment significantly reduced the total fresh biomass by 38% and the total dry biomass by 30%. The fresh and dry BG/AG ratios were not influenced by the water table treatment, which shows that the increased soil water content did not promote water accumulation in the bulb. The fresh and dry BG/AG ratios were not affected by the CO_2 concentration. The leaves of radish began to show signs of chlorosis and stunted growth in the eCO_2 treatment as the harvest date approached (Fig. 2.6). This was especially evident in the eCO_2 -30 cm treatment.

Wet total biomass	**df**	**F-value**	**P-value**
CO_2 level	1, 20	13.32	**0.002 ****
Water table	1, 20	44.87	**<0.001 *****
Water table*CO_2	1, 20	2.03	0.17
Wet mean bulb			
CO_2 level	1, 20	12.2	**0.002 ****
Water table	1, 20	40.28	**<0.001 *****
Water table*CO_2	1, 20	1.28	0.272
Wet mean leaf			
CO_2 level	1, 20	9.22	**0.007 ****
Water table	1, 20	33.79	**<0.001 *****
Water table*CO_2	1, 20	2.86	0.107
Wet mean root			
CO_2 level	1, 20	3.68	0.069
Water table	1, 20	6.12	**0.022 ***
Water table*CO_2	1, 20	2.54	0.127
Dry total biomass			
CO_2 level	1, 20	8.76	**0.008 ****
Water table	1, 20	24.86	**<0.001 *****
Water table*CO_2	1, 20	3.08	0.095
Dry mean bulb			
CO_2 level	1, 20	9.8	**0.005 ****
Water table	1, 20	15.74	**0.001 *****
Water table*CO_2	1, 20	2.08	0.165
Dry mean leaf			
CO_2 level	1, 20	4.04	0.058
Water table	1, 20	23.11	**<0.001 *****
Water table*CO_2	1, 20	2.5	0.13
Dry mean root			
CO_2 level	1, 20	3.42	0.079
Water table	1, 20	9.82	**0.005 ****
Water table*CO_2	1, 20	4.41	**0.049 ***
BG/AG ratio (wet)			
CO_2 level	1, 20	0	0.955
Water table	1, 20	1.44	0.244
Water table*CO_2	1, 20	0.14	0.711
BG/AG ratio (dry)			
CO_2 level CO_2	1, 20	0.86	0.364
Water table	1, 20	1.67	0.211
Water table*CO_2	1, 20	0.03	0.872

Table 2.2: Effects of water table and CO_2 concentration on dry and wet total, leaf, bulb, root biomass and dry and wet BG/AG ratio. BG/AG ratio is the ratio of belowground (roots and bulbs) to aboveground (leaves) biomass weight.

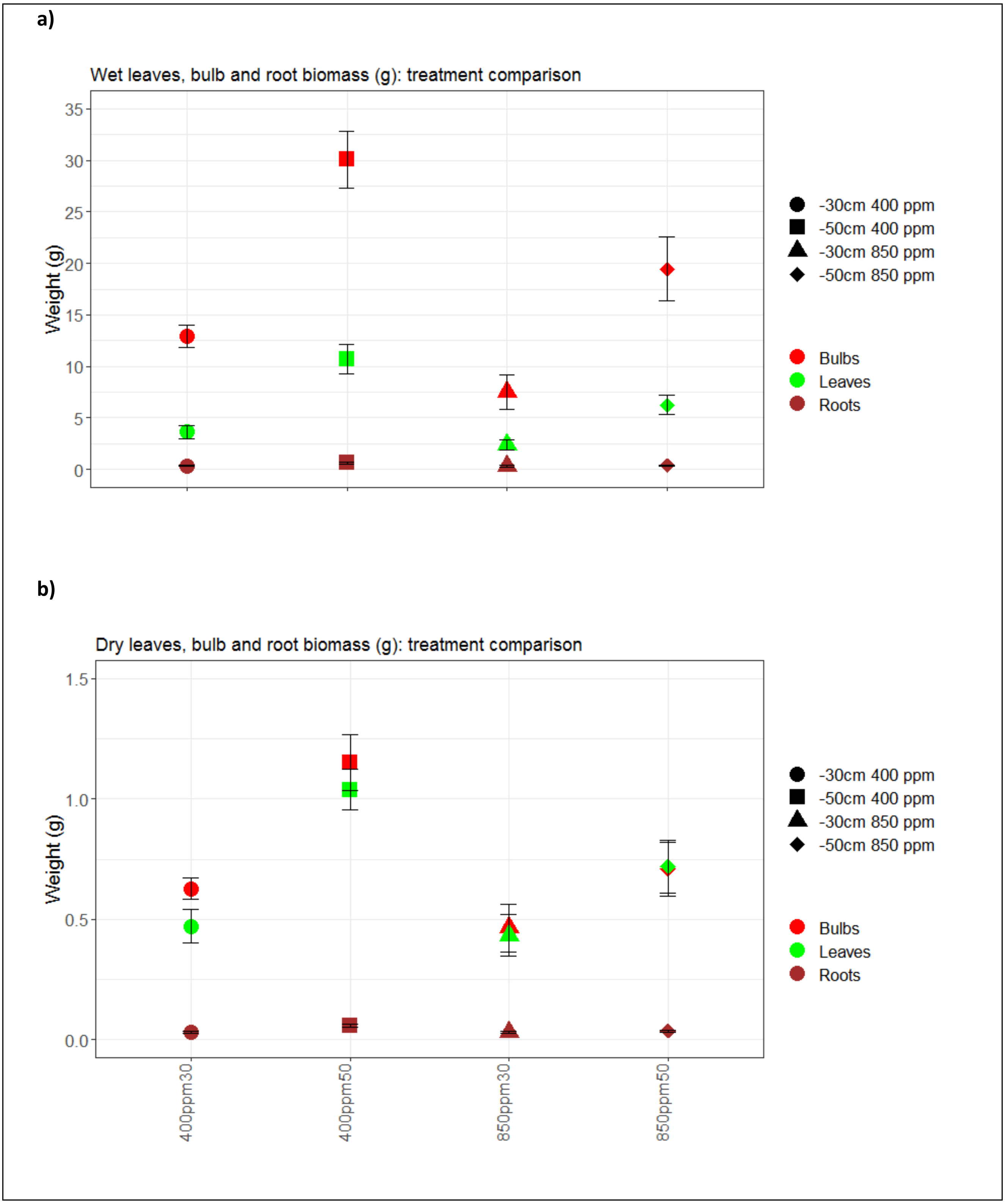


Figure 2.5: Fresh (a) and dry (b) radish bulb, leaf and root biomass. Mean ± 1 standard error. There are two water table levels (-30 cm and -50 cm) and two CO_2 concentration levels (400 ppm-ambient and 850 ppm-elevated).

a)

b)

c)

d)

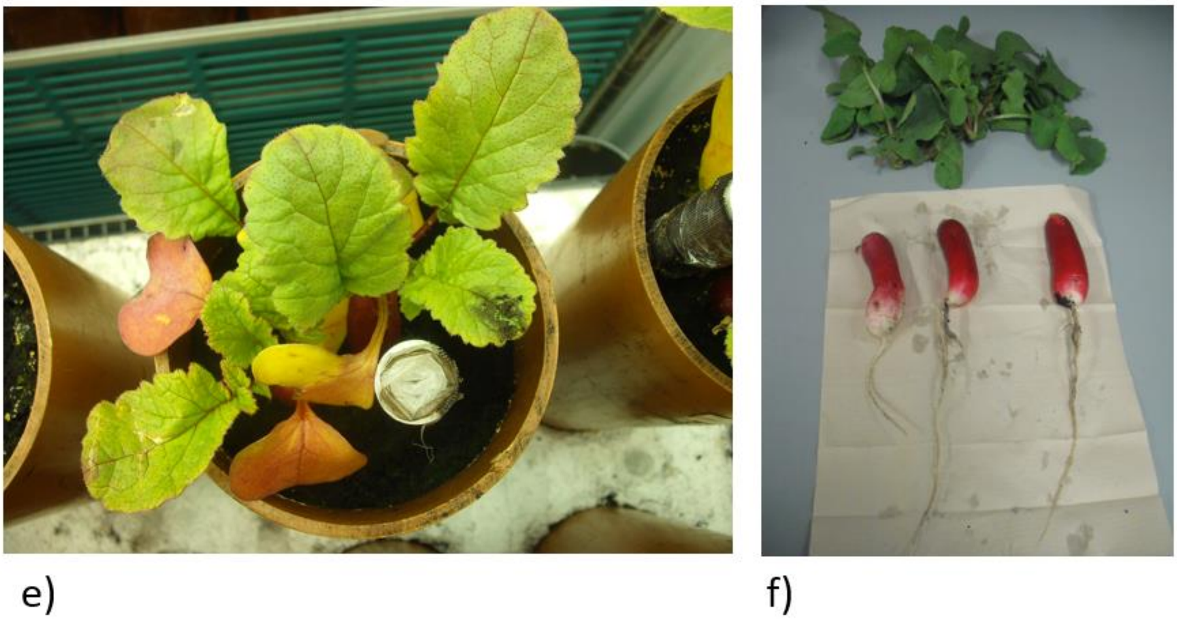


Figure 2.6: Radish plants in their final week of growth under two water table and two CO_2 treatments. a) Ambient CO_2 -50 cm b) Ambient CO_2 -30 cm c) Elevated CO_2 -50 cm d) Elevated CO_2 -30 cm e) Chlorosis in radish leaves grown in elevated CO_2 f) Harvested radish.

2.3.3 Plant and peat C/N ratio, NO_3^- and NH_4^+ content in peat

The leaf C/N ratio was significantly higher in the eCO_2 conditions (by 40%) and in the -30 cm water table (by 78%) (Table 2.3, Fig. 2.7). The leaf C/N ratio was driven by changes in the N content as the C content was not affected by any of the treatments (Table 2.3). The topsoil C/N ratio was not affected by the water table level and the CO_2 concentration in the planted cores, however, in the unplanted cores it was significantly higher (by 3%) in the aCO_2 treatment (as the N content was 2% lower) (Fig. 2.7). The water table depth had no effect on the topsoil C/N ratio of the unplanted cores. The content of NO_3^- and NH_4^+ in peat of the planted cores did not vary between the two water table levels and the two CO_2 concentrations (Table 2.3, Fig. 2.8).

C/N ratio (leaf)	**df**	**F-value**	**P-value**
CO_2 level	1, 19	14.91	**0.0012 ****
Water table	1, 19	43.14	**<0.001 *****
Water table*CO_2	1, 19	9.06	**0.007 ****
Leaf N content (%)			
CO_2 level	1, 19	6.22	**0.022 ***
Water table	1, 19	21.87	**<0.001 *****
Water table*CO_2	1, 19	0.88	0.36
Leaf C content (%)			
CO_2 level	1, 19	0.66	0.428
Water table	1, 19	1.77	0.199
Water table*CO_2	1, 19	0.1	0.754
Topsoil C/N ratio (unplanted)			
CO_2 level	1, 12	8.67	**0.012 ***
Water table	1, 12	0.3	0.597
Water table*CO_2	1, 12	4	0.069
Topsoil C/N ratio (planted)			
CO_2 level	1, 12	0.71	0.415
Water table	1, 12	0.01	0.944
Water table*CO_2	1, 12	1.07	0.321
Topsoil N % (unplanted)			
CO_2 level	1, 12	8.33	**0.014 ***
Water table	1, 12	0.65	0.435
Water table*CO_2	1, 12	6.25	**0.028 ***
Topsoil N % (planted)			
CO_2 level	1, 12	1.49	0.25
Water table	1, 12	0.54	0.47
Water table*CO_2	1, 12	9.27	**0.01 ***
Topsoil NO_3^- (planted)			
CO_2 level	1, 11	0.17	0.687
Water table	1, 11	1.46	0.253
Water table*CO_2	1, 11	0.02	0.893
Topsoil NH_4^+ (planted)			
CO_2 level	1, 11	0.53	0.483
Water table	1, 11	0.47	0.506
Water table*CO_2	1, 11	0.25	0.625
Deep soil NO_3^- (planted)			
CO_2 level	1, 11	1.57	0.236
Water table	1, 11	0.74	0.408
Water table*CO_2	1, 11	0.05	0.82
Deep soil NH_4^+ (planted)			
CO_2 level	1, 11	0.49	0.499
Water table	1, 11	1.87	0.199
Water table*CO_2	1, 11	0.45	0.515

Table 2.3: Effects of water table and CO_2 concentration on leaf and topsoil C/N ratio, topsoil N content, leaf C and N content and topsoil and deeper soil NO_3^- and NH_4^+ content. Topsoil: 0-5 cm depth; deep soil: 30-30 cm depth. All analyses were performed on dried samples.

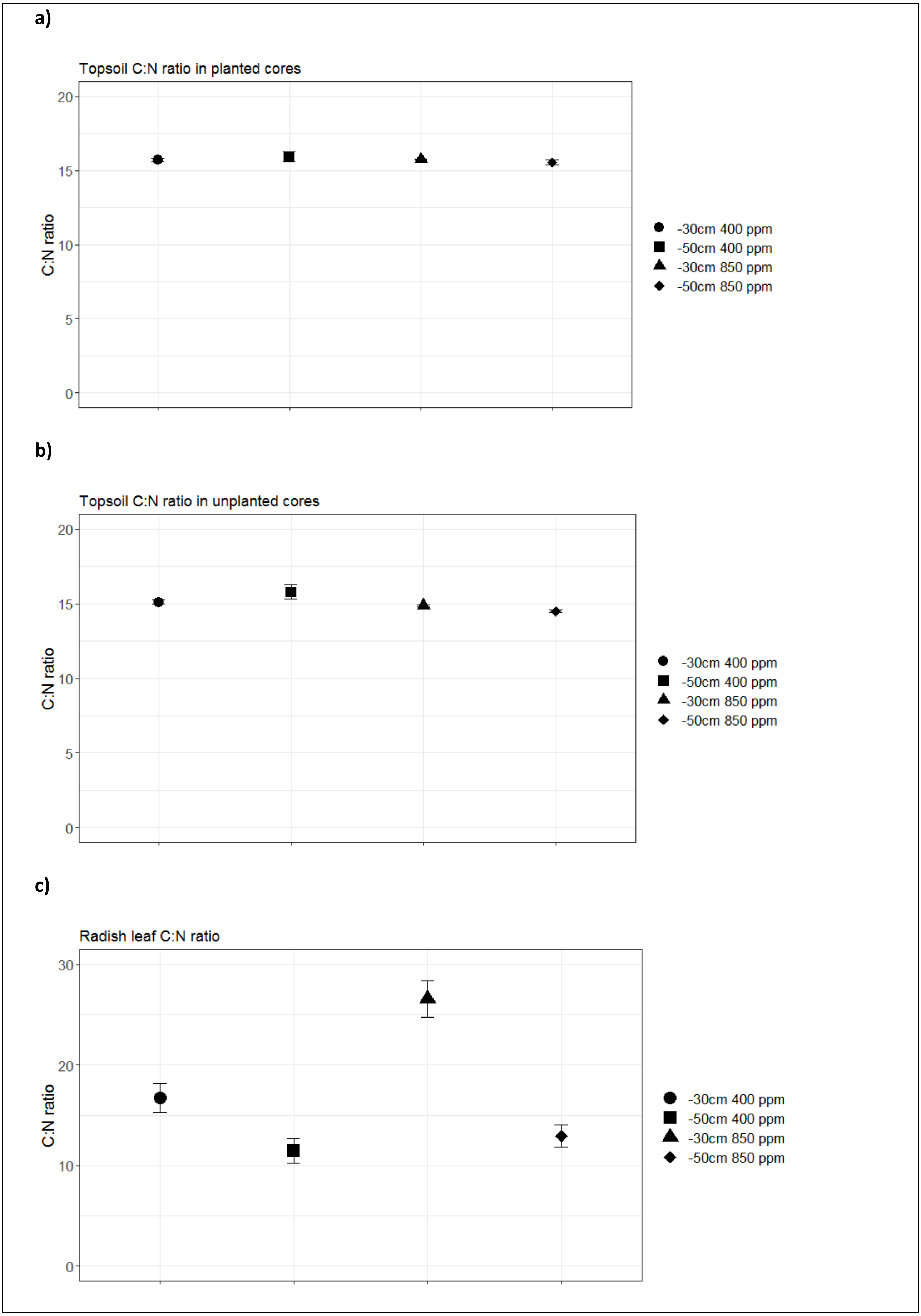

a)
Topsoil C:N ratio in planted cores
C:N ratio
0
5
10
15
20
● -30cm 400 ppm
■ -50cm 400 ppm
▲ -30cm 850 ppm
◆ -50cm 850 ppm
b)
Topsoil C:N ratio in unplanted cores
C:N ratio
0
5
10
15
20
● -30cm 400 ppm
■ -50cm 400 ppm
▲ -30cm 850 ppm
◆ -50cm 850 ppm
c)
Radish leaf C:N ratio
C:N ratio
0
10
20
30
● -30cm 400 ppm
■ -50cm 400 ppm
▲ -30cm 850 ppm
◆ -50cm 850 ppm

Figure 2.7: Plant and soil C:N ratio. Mean ± 1 standard error. Topsoil – 0-5 cm depth. a) Topsoil C:N ratio in planted cores; b) topsoil C:N ratio in unplanted cores; c) radish leaf C:N ratio.

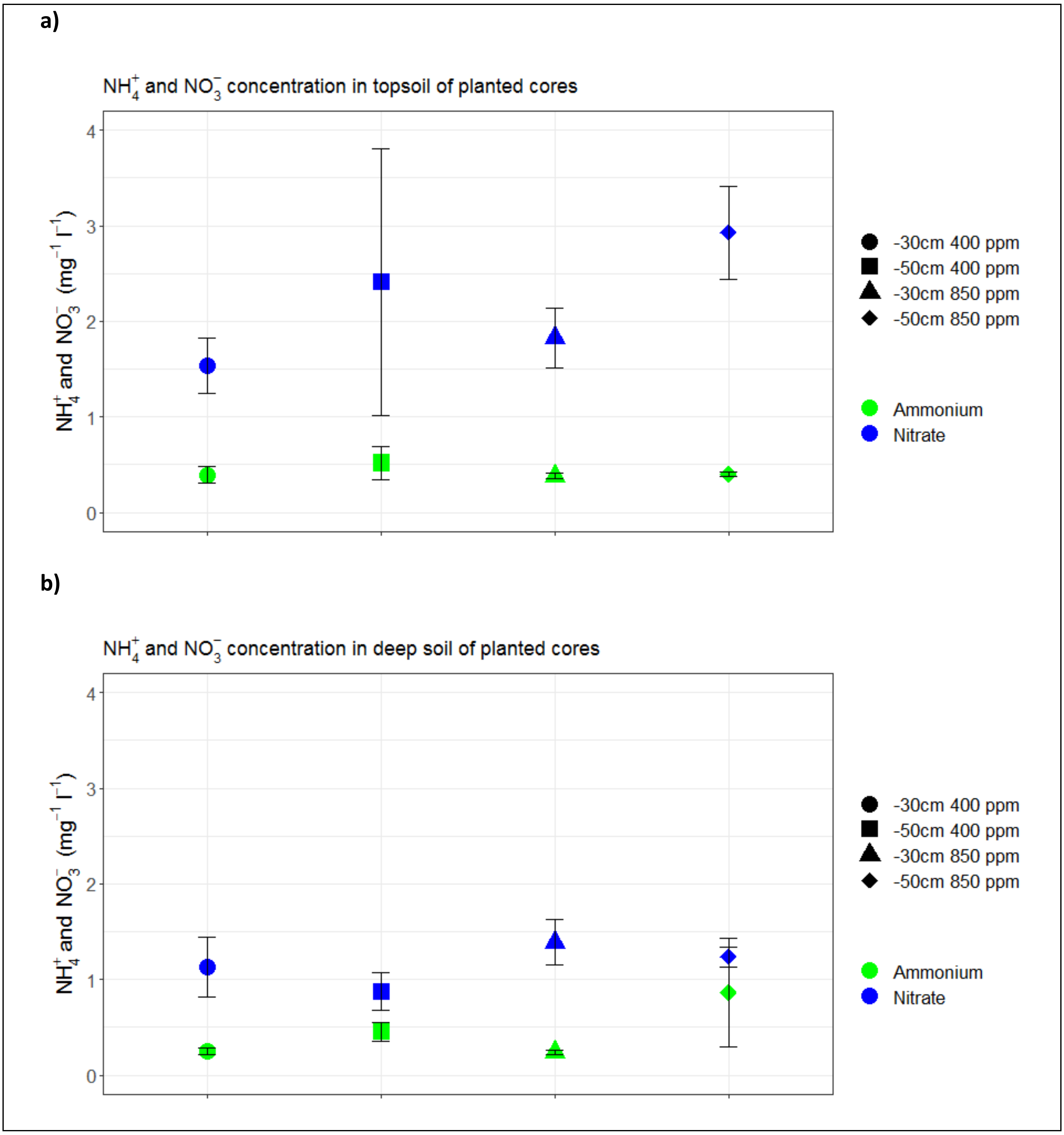


Figure 2.8: NH_4^+ (ammonium) and NO_3^- (nitrate) content in topsoil (a) and deeper soil (b) of planted cores. Mean ± 1 standard error. Topsoil – 0-5 cm; deep soil – 30-35 cm.

2.3.4 Concentrations of mineral nutrients and potentially phytotoxic elements in radish leaves

The concentrations of Al, Cd, Cu and Pb in the radish leaves were at or below the detection limit. There was no difference in the leaf content of Ca, Fe, Mg, Mn, P, S and Zn between the two CO_2

treatments (Table 2.4). Potassium was significantly (60%) lower in the eCO_2 treatment. The concentrations of Ca, Fe, Mg, Mn, P and S were significantly higher (by 19%, 32%, 30%, 21%, 26% and 27%, respectively) in the leaves of plants grown in the -50 cm water table as compared to the -30 cm water table, however, increasing the water table had no effect on the leaf content of K and Zn. The higher water table drastically lowered the leaf concentration of P under the eCO_2 conditions, however, in the aCO_2 treatment the decrease in P was less pronounced. There was a significant positive relationship between soil water content in the top 12 cm of peat and concentrations of Ca, P and S in the leaf biomass, but no influence of soil water content on Fe, K, Mg, Mn and Zn (Table 2.4).

	df	**F-value**	**P-value**
Fe			
CO_2 level	1, 20	0.24	0.627
Water table	1, 20	6.37	**0.02 ***
Water table*CO_2	1, 20	2.96	0.101
Soil water content	1, 22	4.16	0.054
Ca			
CO_2 level	1, 20	0.05	0.826
Water table	1, 20	9.2	**0.007 ****
Water table*CO_2	1, 20	3.4	0.08
Soil water content	1, 22	6.14	**0.021 ***
K			
CO_2 level	1, 20	29.84	**<0.001 *****
Water table	1, 20	3.38	0.081
Water table*CO_2	1, 20	3.49	0.076
Soil water content	1, 22	2.26	0.147
S			
CO_2 level	1, 20	0.13	0.72
Water table	1, 20	8.26	**0.009 ****
Water table*CO_2	1, 20	0.11	0.745
Soil water content	1, 22	11.92	**0.002 ****
Mn			
CO_2 level	1, 20	2.92	0.103
Water table	1, 20	4.81	**0.04 ***
Water table*CO_2	1, 20	0.09	0.768
Soil water content	1, 22	0.94	0.343
Mg			
CO_2 level	1, 20	1.91	0.182
Water table	1, 20	5.3	**0.032 ***
Water table*CO_2	1, 20	2.09	0.164
Soil water content	1, 22	3.11	0.092
P			
CO_2 level	1, 20	0.07	0.793
Water table	1, 20	8.66	**0.008 ****
Water table*CO_2	1, 20	6.52	**0.019 ***
Soil water content	1, 22	8.52	**0.00795 ****
Zn			
CO_2 level	1, 20	1.13	0.301
Water table	1, 20	3.43	0.079
Water table*CO_2	1, 20	0.32	0.577
Soil water content	1, 22	1.82	0.191
Cl			
CO_2 level	1, 19	1.45	0.243
Water table	1, 19	0.01	0.924
Water table*CO_2	1, 19	1.15	0.298
Soil water content	1, 21	0.02	0.893

Table 2.4: Effects of water table, soil water content and CO_2 concentration on leaf content of Fe, Ca, K, S, Mn, Mg, P, Zn, Cl. The total number of samples was n=24 for the ICP-MS analysis (all elements except for Cl) and n=23 for the X-Ray Fluorescence analysis (Cl only).

2.3.5 Peat GHG emissions

Soil respiration was significantly lower (a decrease of 48%) in the -30 cm water table treatment (Table 2.5, Fig. 2.9). There was a significant negative relationship between soil water content and Rh and a significant positive one between soil temperature and Rh (Table 2.5). There was no link between Rh and soil N content. Soil respiration was significantly higher (by one-third) in the eCO_2 chamber. There was no difference in NEE and GPP values between the two CO_2 treatments (Fig. 2.10, Fig. 2.11). The linear model showed less negative NEE and lower GPP in the -30 cm water table treatment. In the linear mixed model the relationship between NEE and GPP and the water table depth was absent (Table 2.5). Ecosystem respiration was not affected by the water table and CO_2 treatments in the mixed effects model (Table 2.5, Fig. 2.12). In the linear model the rates were significantly lower from the eCO_2 and -30 cm treatments. There was also an interaction between the CO_2 level and the water table depth. The disparity in outcomes between the linear models and the linear mixed models is a consequence of the amount of information contained by each model: the GHG fluxes were sensitive to the duration of the experiment (time factor), which was included in the linear mixed models, but not in the linear models. It can be seen in the figures that the values of NEE, GPP and ER were similar between the treatments in the first weeks of the experiment and started to diverge later on (Fig. 2.9-2.12). This implies that the photosynthetic activity of radish was affected by the water table depth only in the final stage of growth, at the time when the plant was ready for harvest. As the yield was significantly lower from in higher water table treatment, the later stages of growth must have been critical for biomass accumulation. The lowered ability to absorb atmospheric CO_2 in the -30 cm treatment is reflected in the biomass: the leaves, root and bulbs had a lower weight.

	lmer			lm		
CH_4	**df**	**χ2**	**P-value**	**df**	**F-value**	**P-value**
Planting	1	0.05	0.826	1, 38	1.78	0.19
Water table	1	20.73	**<0.001 *****	1, 38	34.44	**<0.001 *****
Soil water content	1	17.54	**<0.001 *****	1, 44	26.42	**<0.001 *****
Water table*Planting	1	5.91	**0.015 ***	1, 38	0.02	0.881
CO_2 level	1	3.01	0.083	1, 15	16.57	**0.001 ****
Water table*CO_2	1	1.54	0.215	1, 15	0.3	0.589
Soil respiration (Rh)						
Water table	1	7.2	**0.007 ****	1, 19	23.05	**<0.001 *****
Soil water content	1	0.24	0.622	1, 19	22.24	**<0.001 *****
Topsoil N (%)	-	-	-	1, 14	2.12	0.167
Soil temperature (-10 cm)	1	36.87	**<0.001 *****	1, 19	9.37	**0.006 ****
CO_2 level	1	4.28	**0.039 ***	1, 18	7.24	**0.015 ***
NEE						
CO_2 level	1	0.34	0.561	1, 15	0.95	0.345
Water table	1	2.32	0.128	1, 15	17.2	**0.001 *****
Soil water content	1	0.01	0.918	1, 17	5.45	**0.032 ***
Leaf N (%)	-	-	-	1, 19	5.96	**0.025 ***
Water table*CO_2	1	0	0.978	1, 15	1.59	0.227
GPP						
CO_2 level	1	0.11	0.735	1, 15	1.18	0.294
Water table	1	0.63	0.429	1, 15	24.8	**<0.001 *****
Soil water content	1	0	0.944	1, 17	8.2	**0.01 ***
Water table*CO_2	1	1.82	0.177	1, 15	0.77	0.395
ER						
CO_2 level	1	0.26	0.613	1, 15	7.3	**0.016 ***
Water table	1	0.09	0.769	1, 15	16.14	**0.001 ****
Soil water content	1	0.36	0.547	1, 17	4.47	**0.049 ***
Water table*CO_2	1	2.78	0.095	1, 15	6.6	**0.021 ***

Table 2.5: Effects of environmental variables on gas fluxes. The total number of measurements used in the lmer model was n=276 (for CH_4 in all cores), n=180 (for Rh) and n=96 (for ER, NEE, GPP and CH_4 in planted cores). Rh – soil respiration; NEE – Net Ecosystem Exchange; GPP – Gross Primary Production; ER – ecosystem respiration. lmer -linear mixed models (with ‘week’ and ‘core’ as random effects), lm – linear models (performed on data averaged across time).

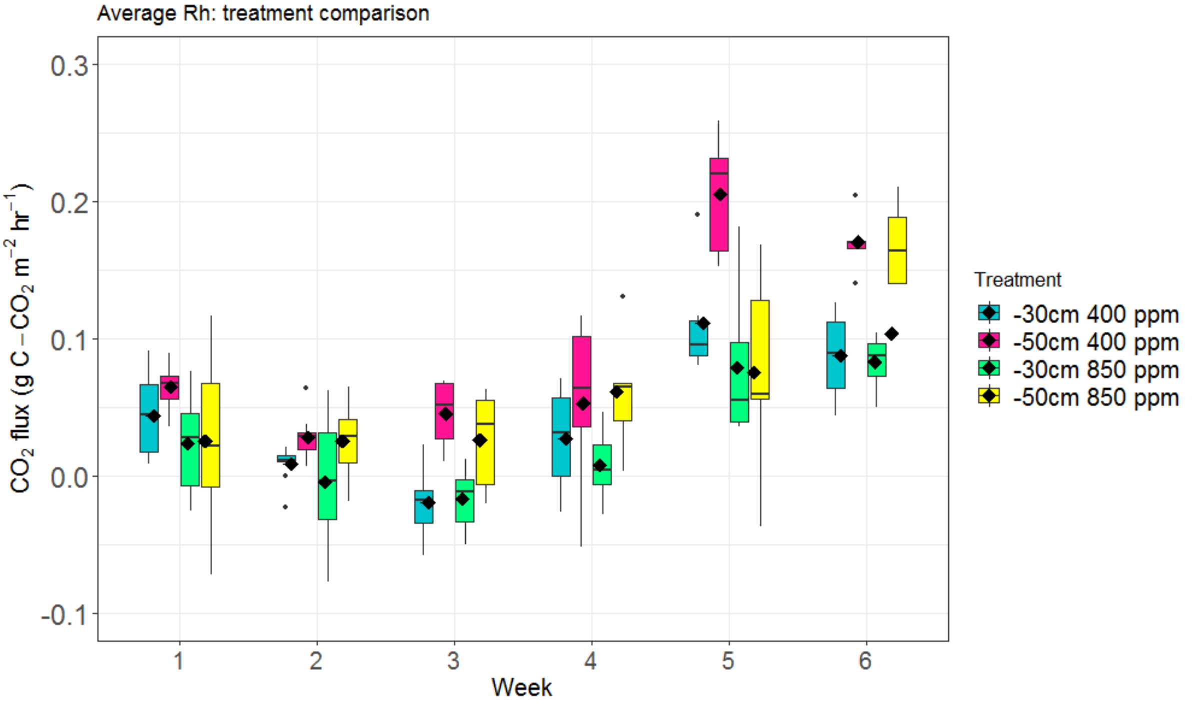


Figure 2.9: Average weekly Rh (soil respiration) from two water table depths (-30 cm and -50 cm) and two CO_2 levels (400 ppm and 850 ppm).

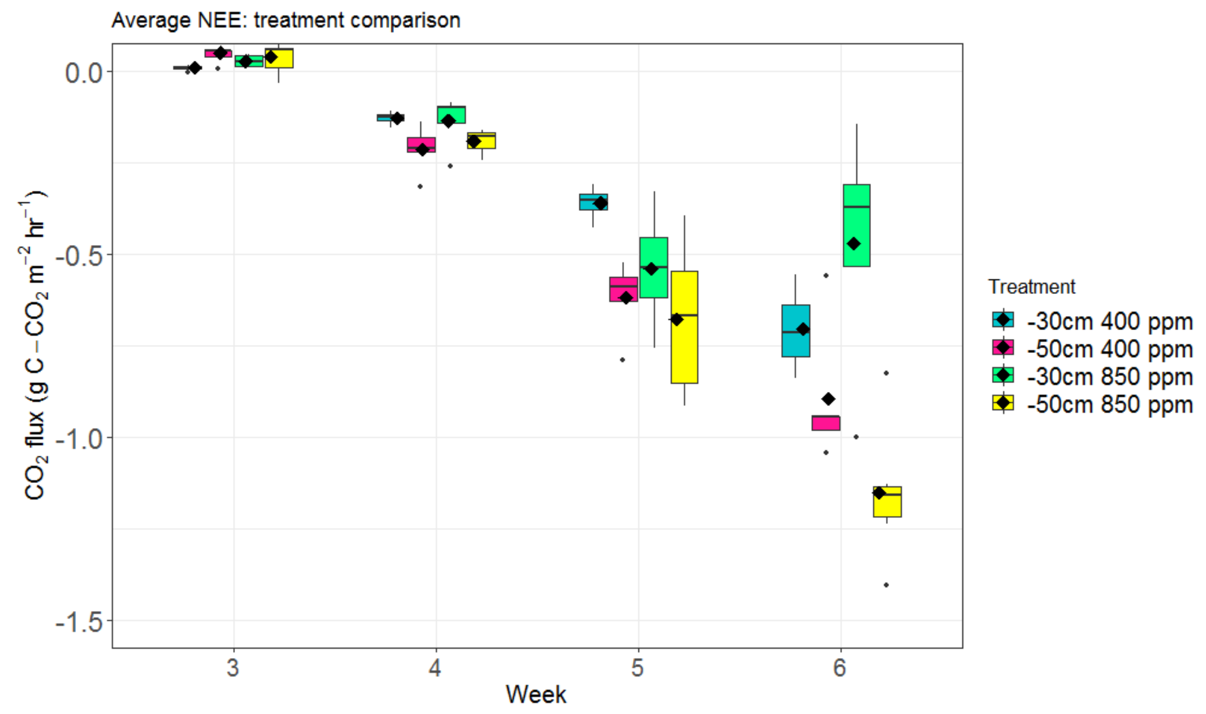


Figure 2.10: Average weekly NEE (Net Ecosystem Exchange) from two water table depths (-30 cm and -50 cm) and two CO_2 levels (400 ppm and 850 ppm).

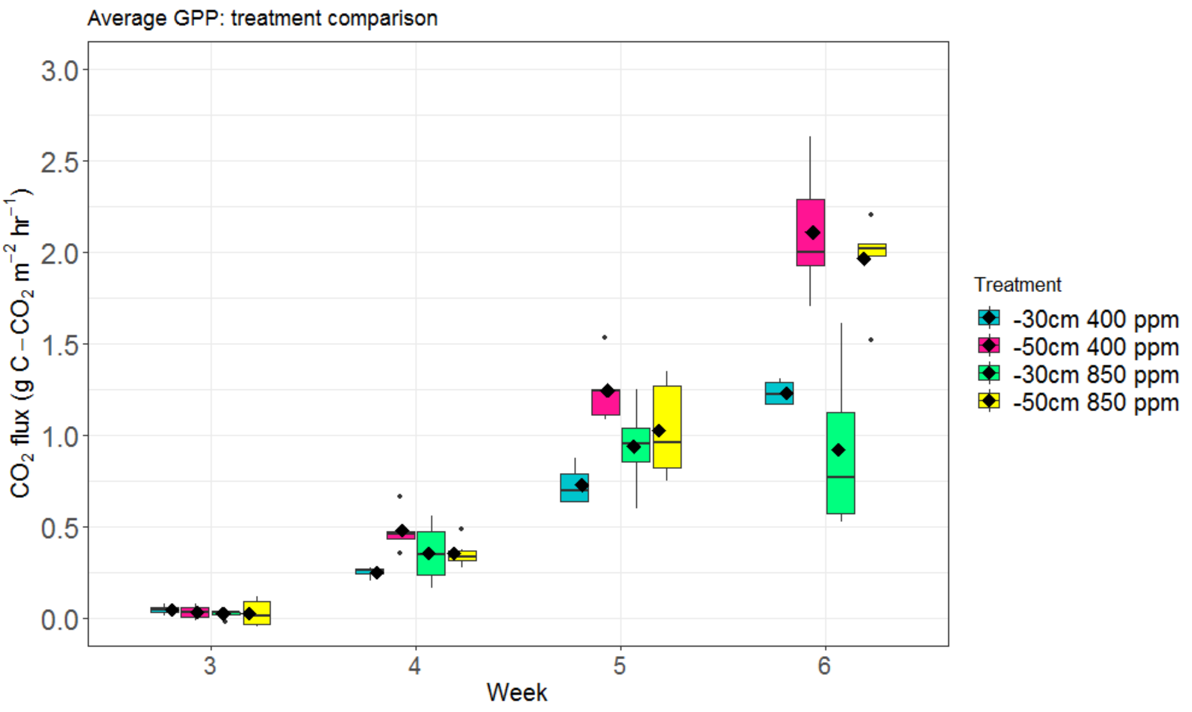


Figure 2.11: Average weekly GPP (Gross Primary Production) from two water table depths (-30 cm and -50 cm) and two CO_2 levels (400 ppm and 850 ppm).

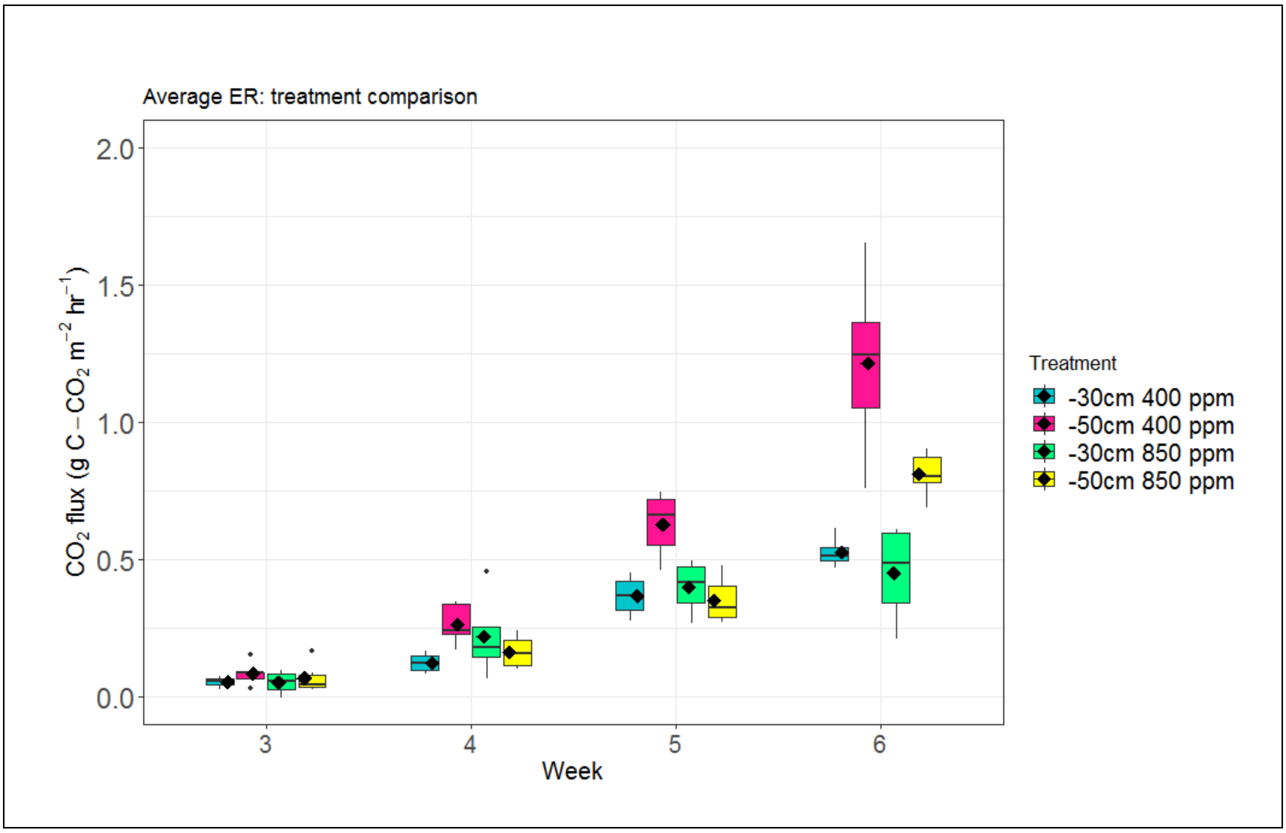


Figure 2.12: Average weekly ER (ecosystem respiration) from two water table depths (-30 cm and -50 cm) and two CO_2 levels (400 ppm and 850 ppm).

Only 40% of the recorded CH_4 values were positive (CH_4 emissions). There was a significant effect of the water table on CH_4 emissions: CH_4 uptake dominated in the -50 cm treatment, whereas in the -30 cm treatment CH_4 release was dominant (Table 2.5, Fig. 2.13). Raising the water table more than doubled the CH_4 flux. There was a significant positive relationship between the CH_4 flux and soil water content. There was no effect of planting on CH_4 emissions, however, the mixed effects model showed a significant interaction between the crop presence and the water table position: cropping in combination with the -30 cm water table resulted in the highest positive fluxes. The mixed linear model showed no effect of the eCO_2 treatment on CH_4 emissions from the planted cores, however, in the linear model the eCO_2 conditions significantly increased CH_4 release (by 73%).

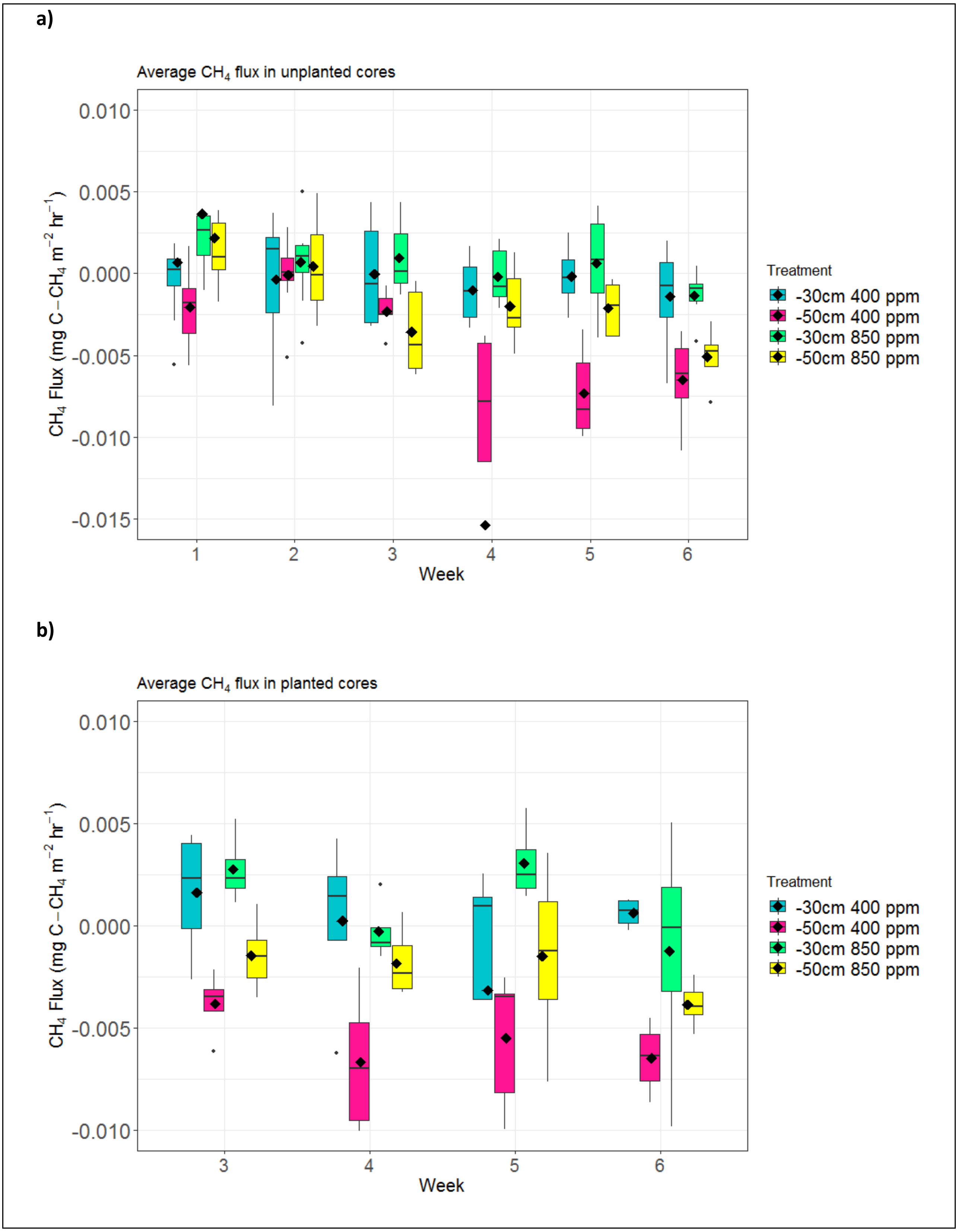


Figure 2.13: Average weekly CH$_4$ flux in unplanted (a) and planted (b) cores from two water table depths (-30 cm and -50 cm) and two CO$_2$ levels (400 ppm and 850 ppm).

2.4 Discussion

2.4.1 Growth conditions

Soil water content was significantly affected by the presence of radish in the linear mixed model, however, not in the linear model: this difference is most likely due to the linear mixed model being sensitive to the time element. In the early stages of growth, radish did not uptake as much water as in the later stages. The uncropped cores did not show any variation in soil water content between the two chambers. On the other hand, the planted cores had higher water content in the eCO_2 chamber: this could be attributed to poorer growth of radish, and so, lesser ability to uptake water. Photosynthetically active radiation was significantly higher in the eCO_2 chamber when compared to the aCO_2 chamber, although the mean difference was not large (33 μmol), therefore it could not have affected the growth of radish and its photosynthetic parameters (Fan et al., 2013; Ferreira et al., 2014).

2.4.2 Effects of raising the water table

The reductions in the radish biomass in the higher water table which were seen in all plant organs (leaves, bulbs and roots) contrast with the findings of Murisaka et al., (2017). Previous studies showed that over-wetting, and especially saturation of soil, can supress plant growth, and this effect can persist even after the excessive water has gone (Gu et al., 2019). Waterlogging can lead to biochemical and microbiological changes in soil, such as shifts in the composition and activities of enzymes as well as anaerobic production of organic and inorganic phytotoxins. Consequently, waterlogging conditions are detrimental to proper growth and development of plants which lack adaptive mechanisms (such as an aerenchyma). Plants react by decreasing or terminating growth and leaf yellowing (chlorosis); leaf abscission and epinasty may occur (Drew and Sisworo, 1977; Drew and Lynch, 1980). Soil anoxia can lead to anaerobic metabolism in roots, which, apart from not generating enough energy for cellular maintenance, results in production of toxic by-products, such as ethanol and acetaldehyde, in the root itself (Drew and Lynch, 1989; Marschner, 2012). Consequently, the stressed plant cannot use as much energy for root and shoot growth and ion uptake and transportation, consequently, becoming nutrient-starved (Foy et al., 1978; Drew and Lynch, 1980). Partial pressure of soil CO_2 increases in anaerobic conditions, which can be detrimental to roots (Shabala, 2011). Phloem transportation is impaired and cell membrane integrity is compromised, leading to leakage of cell contents (Drew and Lynch, 1980). Paradoxically, overabundance of water leads to root desiccation as permeability of roots falls (Drew and Lynch, 1980). Changes in soil enzymes, whose activity is linked to mineralisation of nutrients, may occur: this has consequences for nutrient uptake (Pulford and Tabatabai, 1988; Gu et al., 2019).

Under anaerobiosis, microbial metabolic processes in roots as well as in soil produce compounds such as ethanol, ethylene, acetaldehyde and short-chain aliphatic acids, which are phytotoxic (Drew and Lynch, 1980; Shabala, 2011; Gu et al., 2019). Additionally, elements which were previously locked in forms unavailable for root uptake become reduced to the ionic (available) form under anaerobic conditions (Shabala, 2011). What follows is increased root absorption of metals such as Mn, Fe and Al that are detrimental to plant functions in excess. Concentrations of heavy metals in shoots of waterlogged plants are often found to be above the critical levels for toxicity (Loeb et al., 2008; Setter et al., 2009; Shabala, 2011; Huang et al., 2015; Matsuo et al., 2017). Phytotoxic compounds (such as aliphatic and phenolic acids, ethanol and excessive concentrations of metal cations) can affect the plant by disrupting cell membrane integrity and lowering energy supply to roots (both of which limit the ability to exclude harmful compounds and prevent leakage of cell contents) (Drew and Lynch, 1989; Kirk, 2004; Setter et al., 2009). Symptoms of accumulation of toxins in plants may be diverse, crop-specific and very similar to those of nutrient deficiency (Foy et al., 1978; Kirk, 2004). For instance, in the case of Mn, leaf chlorosis and necrosis may occur (Foy et al., 1978; El-Jaoual and Cox, 1998). However, in the present study the patterns of biomass allocation and the shoot concentrations of potentially toxic elements provide no compelling evidence that these factors contributed to the yield reduction seen with the raised water table. The content of heavy metals (Al, Cd, and Pb) in leaf material was below the limit of detection, but it remains possible that plant growth in the -30 cm treatment might have been negatively affected by other phytotoxic products of anaerobic conditions. The yield reduction was most pronounced for the leaves, suggesting that direct toxicity to roots was probably not the primary constraint on growth.

In aerated conditions, compounds previously reduced (=available for root absorption) become re-oxidised (making them unavailable) (Dowrick et al., 2006; Knorr et al., 2009). It is not clear how much time is required for complete oxidation of products of reduction in peat following drainage, and thus at what concentrations phytotoxins remained in the peat cores over the period of this experiment. The key factor which could be used as a proxy is the redox potential and research suggest that redox conditions in soil could potentially last for prolonged periods of time after the water table is lowered. Lynch (1978) noted that degradation of acetic acid which accumulated in water-saturated peaty, loamy and clay soils took a few days following drainage. Setter et al. (2009) showed that low redox conditions were still present in sandy soils ten days after drainage (when the last measurement was made) and likely continued for longer. Loeb et al. (2008) reported that in fluvisol the return of Mn^{2+} and Fe^{2+} (two products of reduced conditions) values to pre-flooding levels occurred over a period of two weeks at temperatures of around 20°C. Knorr et al. (2009) noted that anaerobic zones could be still present in peat above the water table level even during drought. Rubol et al. (2012) showed that the redox potential in peat at a -80 cm depth rebounded in a couple of days to pre-flooding values, but at a -20 cm depth it remained static at values lower than before throughout twenty days after drainage. Additionally, they also showed that recovery of oxygen concentrations to pre-flooding levels at depth of -108 cm took more than twenty days (Rubol et al., 2012). Their study demonstrated that the redox potential in the period after drainage was higher at depth when compared to the topsoil, even though oxygen content was significantly lower at depth during and after flooding, which is a surprising finding (Rubol et al., 2012). On the other hand, Niedermeier and Robinson (2007) showed that differences in redox potential at depths of -10 cm, -30 cm, -60 cm and -90 cm were minimal on a fen site. Niedermeier and Robinson (2007) noted that the increase in the redox potential at the -10 cm depth following drainage was characterised by sharp spikes, rather than gradual recovery, and could take up to a month in summer conditions of the UK. In marine gleysol redox potential at a -10 cm depth varied very little with changes in the water table position (which fluctuated between -33 cm to below -200 cm), however, at a -60 cm depth the fluctuations were quite sharp (from -200 mV to 700 mV) (Mansfeldt, 2003). Typically, in cultivated ecosystems bulk density increases and hydraulic conductivity decreases with the degree of peat degradation (Hallema et al., 2015; Liu and Lennartz, 2019), which has consequences on soil aeration. The extent of regeneration of oxygen penetration post-rewetting could be controlled by the water table position and bulk density: higher water table levels and higher bulk density values tended to result in lower oxygen concentrations in degraded peat (Estop- Aragonés et al., 2013). Recovery of oxygen concentrations in topsoil took only a couple of days following rewetting events which resulted in water table increases to a maximal depth of -10 cm, however, it was slow or non-existent in plots with high bulk density (Estop-Aragonés et al., 2013). Given that drained agricultural peats undergo accelerated degradation which leads to higher bulk density, there is enough of a basis to suspect that some products of reduced conditions were still present in the peat cores during the growth of radish.

Limited uptake of essential nutrients (N, Fe, Ca, S, Mn, Mg and P) likely contributed to the observed yield reduction. Waterlogging might have limited the depth and extent of the radish roots, restricting access to these nutrients. Moreover, conditions of saturation can have a multitude of effects on N utilisation in crops: N uptake and transportation are hindered and activity of N-metabolising enzymes is reduced, leading to lower NUE (Drew and Lynch, 1980; Ren et al., 2017; Gu et al., 2019). Anaerobic conditions affect the availability and chemistry of soil N.

Soil microorganisms use NO_3^- as an electron acceptor when oxygen is absent (Shabala, 2011). Consequently, NH_4^+ content increases and NO_3^- content falls as losses of NO_3^- through denitrification and leaching are enhanced while nitrification is inhibited: this contributes to NH_4^+ build-up in soil (Fillery and Vlek, 1982; Alaoui-Sosse et al., 2005; Loeb et al., 2008; Gu et al., 2019). However, NH_4^+ may not accumulate at all under anaerobiosis (Boomer and Bedford, 2008) or the increase in NH_4^+ may not be enough to counterbalance the loss of NO_3^-, leading to N deficiency in plant tissues (Alaoui-Sosse et al., 2005). Ammonium may accumulate to toxic concentrations in plant tissues under soil anaerobiosis (Kirk, 2004; Marschner, 2012). Plants vary in NH_4^+ tolerance thresholds and NH_4^+ toxicity typically manifests as leaf chlorosis, growth suppression, a lower root:shoot ratio and deficiency of certain cations (Britto and Kronzucker, 2002; Esteban et al., 2016). Excessive NH_4^+ content may interfere with uptake of Mg, Ca, and K (Gigon and Rorison, 1972; Foy et al., 1978; Britto and Kronzucker, 2002). Plants may exhibit preferences for either NO_3^- or NH_4^+ as their main N source and perform better when N is available in their preferred form (Gigon and Rorison, 1972). In this experiment the radish leaves were visually more chlorotic in the -30 cm treatment likely due to the lower N content in leaf tissue. Nevertheless, there was no difference in the topsoil content of total N, NO_3^- and NH_4^+ between the two water table treatments: this indicates that the limited radish uptake of N in the -30 cm water table was a consequence of poor N absorption rather than deficiency in peat. The fall in the leaf N content with the raised water table was much more drastic in the eCO_2 treatment indicating that conditions of higher soil water content and reduced transpiration and associated mass-flow would inflict more stress on radish (and potentially other crops) grown in peats of the Fens under future high CO_2 concentrations (Taub and Wang, 2008). This is elaborated upon in the following section.

2.4.3 Effects of elevated atmospheric CO_2

Elevated atmospheric CO_2 can have positive effects on assimilation of C, WUE, Nitrogen Use Efficiency (NUE), and also accelerate or delay plant development and alter duration of each growth stage (Gifford, 1977; Sionit et al., 1981; Osanai et al., 2017; Ruiz-Vera et al., 2018; Asif et al., 2018; Uddin et al., 2018; Campbell and Fourqurean, 2018). Faster leaf expansion allows for greater biomass accumulation (Fangmeier et al., 2002; Usuda, H., 2004; Yamakawa et al., 2004). The outcome of this experiment, namely the radish leaf and bulb biomass being lower in the eCO_2 treatment, is an unexpected finding as the vast majority of studies (Idso and Kimball, 1988; Daymond et al., 1997; Wurr et al., 1998) and the previous study on radish by Musarika et al. (2017) report positive or neutral effects of CO_2 fertilisation on crop yield. The results of the leaf elemental analysis suggest that the poor radish growth in the eCO_2 treatment may be nutrient-related. As mentioned in the methodology section, the soil was reused between this experiment and the study by Musarika et al. (2017) (although unused peat was added into previously planted cores) and no fertilisation was applied. This could have created conditions of nutrient limitation in all cores, however, only the eCO_2 plants showed visible signs of nutrient deficiency (leaf discolouration), which would suggest that fertilisation with CO_2 might have been a key factor in uptake and use of certain essential elements. Differences in nutrient uptake and biomass concentration under eCO_2 are reported in a number of studies. In rice, elevated CO_2 resulted in higher biomass and lower concentrations of N, P, K and Mg, with Si and Ca not significantly different in aboveground biomatter (Yamakawa et al., 2004). However, the uptake of these minerals from the growth medium was greater in eCO_2 conditions (Yamakawa et al., 2004). Wheat grown in elevated CO_2 had increased uptake of certain elements and decreased accumulation of others (Fangmeier et al., 1997). Lower concentrations of P, Fe, Zn, Mg were noticed in wheat grain grown at 550 ppm (Erbs et al., 2010). Reaction of nutrient dynamics to elevated CO_2 can also vary between plant functional types and organs: in trees lower leaf N concentration was observed with CO_2 fertilisation, however, crops were found to react to higher

CO_2 levels by increasing N content in leaves and lowering it in roots (Sardans et al., 2016). At 680 ppm CO_2 potato tubers and aboveground shoots had lower N, Mn, Fe and N, K, Mg concentrations, respectively, although the total amount of nutrients absorbed increased (Fangmeier et al., 2002). However, deficiency of specific micro- and macro-elements may produce similar symptoms in crops: it is often not feasible to determine which nutrients were lacking by visually examining the plant. The analysis of the radish leaf material showed that there was no significant difference in concentrations of most elements, apart from K and N, which were significantly lower in the leaves of radish grown in the eCO_2 chamber. Although the concentrations of K and N were significantly lower in the leaves, it does not automatically mean that the radish plants were deficient in these elements: determining the threshold of nutrient deficiency in plant tissue is a contested area and nutrient requirements may vary between species and growth conditions (Morghan, 1985; Chalmers et al., 1999). At eCO_2 values the C/N ratio in plant tissue typically increases as N content falls (Yang et al., 2011). These decreases can be caused by downregulation of the photosynthetic enzyme Rubisco (Uddling et al., 2018), as well as increased synthesis of metabolic products that are typically low in N (Gifford et al., 2000). The lack of a significant difference in the soil C/N ratio and the soil NO_3^- and NH_4^+ concentrations of the planted cores between the two CO_2 treatments in my study suggests that the divergence in N leaf content may not be attributable to variation in the quantity of N in soil.

Taub and Wang (2008) and Mcgrath and Lobell (2013) provide a compilation of theories which attempt to explain decreased content of N in plant biomass under fertilisation with CO_2. I will examine them in relation to the outcomes of this study.

1. Dilution by carbohydrates and other compounds.

A number of studies confirm this phenomenon (Wong et al., 1990; Gifford et al., 2000; McGrath and Lobell, 2013). Under eCO_2, photosynthesis is enhanced, leading to greater accumulation of photoassimilates: the concentration of nutrients falls, however, the total nutrient content in the whole plant does not change or increases. This effect is unlikely to have contributed to differences in nutrient concentrations in my experiment: the biomass of radish was lower in the eCO_2 treatment, meaning that increased accumulation of photoassimilates did not occur.

2. Decreased transpiration leading to lower mass flow.

Greater stomatal closure as a result of CO_2 enrichment leads to decline in transpiration and, consequently, lowers the uptake of those nutrients (such as N, Ca, Mg, S) which are absorbed by roots primarily by mass flow. Whereas this theory would provide the answer to the lower leaf N content in the eCO_2 treatment, it does not explain the depressed leaf K concentration as K is mostly absorbed by diffusion (Marschner, 2012). The significant differences in K content in the radish leaf material suggest that substantial amount of NH_4^+ might have remained in the peat columns after drainage and competed with K cations for root uptake (Gigon and Rorison, 1972; Foy et al., 1978; Britto and Kronzucker, 2002). This effect was more pronounced in planted eCO_2 cores due to higher soil water content. Nevertheless, NH_4^+ in the topsoil and at the –30-35 cm depth did not show a significant difference between the two CO_2 treatments. This could be explained by the fact that the samples were collected at the end of the experiment, when the higher temperature (20°C) and plant maturity (which translates into extensive root penetration) contributed to peat aeration and, consequently, greater rates of nitrification. A depressed rate of transpiration would also manifest as lower redox potential in peat. Consequently, the toxic products of redox conditions would take longer to oxidise following a water table drawdown. Before my experiment began, all cores were preserved by flooding. This might have created the right conditions for the build-up of toxic compounds in peat, additionally, anaerobic zones within peat cores might have persisted throughout the experiment. Not much is known about effects of increasing atmospheric CO_2 concentrations on phytotoxin accumulation in biomass and their distribution between organs of particular crops. The existing research suggests that the effects may be species-dependent. Rice accumulated more Cd in elevated CO_2 in some organs, but not others, and both the low and the high contamination treatments displayed higher plant biomass under eCO_2 as compared to ambient (Li et al., 2010). Elevated CO_2 increased bioaccumulation and concentration of Cd, but decreased concentration of Zn in roots and shoots of wheat (Wang et al., 2016). In elevated CO_2 conditions biomass of rape and common pasture species grown in a substrate with toxic levels of Cu was higher when compared to the ambient treatment, and the response of plant Cu concentrations to the CO_2 treatment varied between species (Tian et al., 2014). Mustard and sunflower plants grown at toxic Cu levels performed better in the eCO_2 treatment (Tang et al., 2003). Fertilisation with CO_2 reduced Cd toxicity in a species of macroalga (Ma et al., 2018b). In wheat, elevated CO_2 alleviated stress conditions caused by Cd contamination via increased enzymatic activity (Jia et al., 2016), but also made the plant less resilient to environmental stress by decreasing biomass content of flavonoids in another study (Jia et al., 2014). Wheat grown in a Cd-contaminated soil displayed greater root secretion of sugars and amino acids, but lesser of phenolic acids in the eCO_2 treatment, which could affect nutrient and microbial dynamics in the rhizosphere, potentially contributing to sustaining microbial communities (which readily consume easily-degradable organic compounds) (Jia et al., 2014).

It is likely that a decline of the transpiration rate occurred in the radish grown under eCO_2 as the soil water content in the planted eCO_2 cores was significantly higher than in the planted aCO_2 cores, while there was no difference in soil water content between the two CO_2 treatments in the unplanted cores. The higher soil water content in the planted cores under CO_2 enrichment might have contributed to presence of pockets of anoxia, whose reducing conditions stored phytotoxins which failed to oxidise. It is likely that absorption of N was impaired by this mechanism, nevertheless, it is not known to what degree, if at all, the decrease in mass flow affected the stock of toxic compounds in peat as these were not measured, aside from the toxic heavy metals (which were below the level of detection in all treatments).

3. Inefficient root architecture and diminished root uptake ability in CO_2-enriched environments.

Changes in root morphology under eCO_2 conditions can make roots less efficient at nutrient uptake (Pritchard and Rogers, 2000). Shallower rooting, more branch roots and more fine root production as well as altered mycorrhizal properties were as possible explanations (Thomas et al., 1999; Pritchard and Rogers, 2000; Alberton et al., 2005), although the exact mechanisms behind the nutrient uptake impairment in roots in conditions of eCO_2 are largely unknown. Nutrient deficiency would typically lead to greater expansion of the rooting system, however, in my experiment neither the dry nor the fresh root biomass differed between the two CO_2 treatments. It is possible that instead of investing more assimilate in the main root, radish plants directed it largely into fine root production as reported by Thomas et al. (1999) in *Pinus* trees (more fine root production at depth at 650 ppm-CO_2 as compared to ambient) and Norby et al. (2004) in a deciduous forest (doubled fine root production at 550 ppm-CO_2). Nevertheless, properties such as root length, distribution, diameter and ability to uptake nutrients were not examined in this study, therefore I cannot be certain whether being subjected to the eCO_2 treatment affected functioning and morphology of the roots of radish.

4. Higher NUE in eCO_2 conditions leading to lower plant demand for N.

According to this hypothesis, lower nutrient content in plant tissues is a result of decreased plant demand as cellular processes become more efficient. Growth and photosynthesis of the plant are not compromised by lower nutrient content in tissues when this mechanism is present. In the case of N, such decreases may be related to falling Rubisco concentrations in leaves as photosynthesis becomes more efficient (Uddling et al., 2018). Concentrations of Mg in photosynthesising tissue may fall following declines in Rubisco as Mg is an important component of the enzyme (Mcgrath and Lobell, 2013). Higher NUE may manifest as increases in the leaf C/N ratio (Curtis, P.S., 1996; Yang et al., 2011; Sardans et al., 2017; Du et al., 2019). However, conditions of eCO_2 may also increase demand for N and P (due to a higher rate of biomass production), which leads to soil nutrient depletion and greater root production as the plant mines for essential elements (Osanai et al., 2017; Cohen et al., 2018; Ma et al., 2018a). In my study, the lower leaf N and K concentrations and the higher leaf C/N ratio under CO_2 fertilisation coincided with the lower total fresh and dry biomass and leaf chlorosis, which would suggest that the radish plants were not faring well as a result of insufficient uptake of these two elements. Additionally, there was a significant positive relationship between the leaf N content and NEE averaged across time, indicating that N could have been the factor limiting photosynthesis (Evans, 1989; Hay and Porter, 2006; Ren et al., 2017). For these reasons, a higher nutrient use efficiency could not have been the driving force behind the lower concentrations of N and K in leaves.

5. Changes to partitioning of nutrients between tissues and organs.

Atmospheric enrichment with CO_2 may alter plant physiology by changing allocation of micro- and macro-nutrients between sinks, possibly favouring reproductive organs (Asif et al., 2018). In wheat grown under K deficiency, CO_2 fertilisation improved grain yield (Asif et al., 2018). However, whereas concentration of K was higher in the grain, it was lower in other plant tissues (leaves, stem) and this tendency was enhanced under eCO_2 (Asif et al., 2018). Unfortunately, it was not possible to determine whether this mechanism was present in my experiment as several bulb samples were missing. Consequently, statistical analyses on bulb mineral content could not be performed.

6. Increased N loss through root exudation.

This process was observed by Pang et al. (2006) in rice, however, it was not the main mechanism behind lower N content in the plant biomass in their study. It is not known whether excessive loss of nutrients via roots was present in my experiment.

It is difficult to state with certainty which factor (nutrient deficiency, increased phytotoxicity, altered root functions or general waterlogging injury) was primarily responsible for the poor appearance and performance of radish in the eCO_2 conditions, although decreased mass flow as a result of fertilisation with CO_2 was most likely involved. There is a need for further comparative studies which would help to build a case of whether there is a disadvantage to crops growing under eCO_2 when soil conditions are less than ideal, especially in peat soils subjected to flooding and fluctuations of the water table.

2.4.4 Effects of elevated CO_2 on biomass sinks

For farmers any possible changes in strength of each individual sink are as important as the effect of rising CO_2 levels on the rate of crop biomass accumulation, since the marketable product is a specific organ, not the plant as a whole. Research shows that allocation of assimilates between different organs in CO_2-enriched conditions varies between species, with crops displaying both decreases, increases and no changes in the root:shoot ratio and in distribution of assimilates between organs in general (Tognoni et al., 1967; Kriedemann et al., 1976; Gifford, 1977; Sionit et al., 1981; Idso et al., 1988; McGranahan and Poling, 2018). CO_2 enrichment was found to strengthen the root sink in carrot at a CO_2 concentration of 640 ppm (Idso et al., 1988), in grapevine at 1200-1300 ppm-CO_2 (Kriedemann et al., 1976), in bean at 1000 ppm-CO_2 (Tognoni et al., 1967), in wheat at 675 ppm-CO_2 and 1000 ppm-CO_2 (Sionit et al., 1981). In wheat, atmospheric CO_2 values of ~500 ppm were shown to improve the dry grain yield (by 43%) (Gifford, 1977), the seed weight and the average number of seeds per plant (Sionit et al., 1981). The root:shoot ratio increased in barley, durum wheat, maize, oats, sorghum, pinto bean and sunflower when CO_2 concentration was 700 ppm (McGranahan and Poling, 2018). In tomato, additional biomass was allocated to leaves and stems, with no effect on fruit weight at a CO_2 level of 590 ppm (Pazzagli et al., 2016). Both the below- and the above-ground biomass and the grain yield of wheat increased when the atmospheric CO_2 concentration was 700 ppm (Uddin et al., 2018). In tropical conditions, raising the CO_2 concentration to 490 ppm increased the aboveground and root biomass, but lowered the grain yield by 6% in rice (Satapathy et al., 2015). The magnitude of the CO_2 fertiliser effect on harvestable crop organs can vary between crops, between the cultivars of a single crop, and will also depend on other environmental factors, such as temperature and soil nutrient status (Daymond et al., 1997; Wurr et al., 1998; Pazzagli et al., 2016; Ma et al., 2016; Ma et al., 2018a). In the study of Pazzagli et al. (2016), dry tomato plant weight was enhanced in 590 ppm CO_2 conditions by 18% in one cultivar and by 9% in another. In common bean the root:shoot ratio under eCO_2 was dependent on soil P availability: at high soil P concentrations the root:shoot ratio increased, whereas it did not change when soil P content was low (Ma et al., 2018a). In this experiment, the lack of significant differences in the root:shoot and the BG/AG ratios between the two CO_2 treatments indicates that no sink was stronger in eCO_2 conditions.

2.4.5 Effects of treatments on GHG emissions

The lower Rh flux in the -30 cm cores shows that raising the water table to -30 cm proved to be a viable option of reducing the rate of peat decomposition. Similar outcomes on agricultural peats were reported by Poyda et al. (2016), Wilson et al. (2016), Peacock et al. (2019), Hemes et al.

(2019), among others. The NEE and GPP fluxes were not affected by the atmospheric CO_2 values, which means that the radish plants from the eCO_2 treatment assimilated as much C as the ones from the ambient chamber, despite their lower leaf biomass and generally poorer visual outlook. Therefore, there is a possibility that the photosynthetic rate on a leaf scale was higher in the eCO_2 treatment, although this cannot be proven as I did not measure LAI. This finding would suggest that the photosynthesis of radish was not constrained and photosynthetic downregulation did not occur under eCO_2, even when the plant suffered from nutrient deficiency. Likewise, it is not possible to state with certainty whether a reduction in stomatal conductance occurred. Soil water content in the planted cores was higher in the eCO_2 chamber: this could be caused by limited transpiration, but also by a lower overall water uptake by the radish plants with lower biomass. The planted cores in the eCO_2 treatment displayed higher CH_4 emissions when compared to their aCO_2 counterparts: this is most likely attributable to the higher soil water content in the planted eCO_2 cores, which limited oxidation of CH_4.

The ER flux was lower in the eCO_2 treatment, which is consistent with other studies incorporating CO_2 fertilisation (Bunce, 1992; Wullschleger et al., 1992; Curtis, 1996; Kubisuke and Pregitzer, 1996). Low ER fluxes under CO_2 enrichment are attributable to changes in leaf tissue chemistry, such as suppression of respiratory enzymes, increased dark fixation of CO_2 and changes in phytomass composition (Amthor, 1991; Wullschleger et al., 1992). A shift in phytomass composition from more complex compounds (such as proteins) to simpler ones reduces growth and maintenance respiration: this manifests as increases in the tissue C/N ratio as protein content falls (Amthor, 1991). A shift in compound composition probably occurred in this study as the leaf C/N ratio was higher in the eCO_2 treatment. A decrease in ER affects C cycling between the plant and the atmosphere, possibly increasing C storage in biomass. However, despite the lower ER and the not significantly different NEE, the radish plants grown in the eCO_2 treatment did not store as much dry and wet biomass as in the aCO_2 conditions. This raises the question of why the net C gain was not evident in the biomass weight. A possible explanation would be excessive loss of the fixed C as root exudates.

The average CH_4 fluxes were positive and negative in the -30 cm and -50 cm treatments, respectively. Several agricultural studies on peat demonstrate that water tables depths as shallow as -20 cm and -30 cm are enough to provide the right conditions for complete CH_4 oxidation (Reno-Wilson et al., 2014; Regina et al., 2015; Karki et al., 2016). Regina et al. (2015) showed that increasing the water table on cultivated peat from -70 cm to -30 cm reduced CO_2 loss by one-third, while keeping CH_4 fluxes negative. Petersen et al. (2012) reported that CH_4 emissions from arable peat (under grain crops, potato and clover-grass) did not depend on seasonal changes in the water table position, with water table levels varying from -10 cm in winter to below -1 m in summer. In contrast with these studies, my experiment proved that CH_4 emissions dominated when the water table was set to -30 cm. The positive CH_4 fluxes in the -30 cm treatment are likely related to the high soil water content in the topsoil, to which capillary rise as well as high water-holding capacity of peat contributed and which was further exacerbated by the simulated flooding (Gnatowski et al., 2002; Hallema et al., 2015). Under such conditions, pockets of anoxia in the topsoil might have been present throughout the duration of the experiment, preventing oxidation of CH_4. Although positive, the emissions of CH_4 were very low, which is in line with what is reported by Poyda et al. (2016) on peat under grassland at mean water table levels of -25 cm and lower. Root exudation may increase methanogenic activity in soil (Green et al., 2014), however, the lack of an effect of the radish presence on CH_4 emissions suggests that radish root exudates did not stimulate nor supress the activity of methanogenic communities.

The difference in outcomes in GHG flux analysis between the linear models and the linear mixed models could be attributed to the quantity of information contained in each model type. The linear mixed model contains more information (as it takes into account the changes in GHG emissions with time, as the temperature is gradually being increased and plants become larger), unlike the linear model, which utilises flux data averages from the whole duration of the experiment. As seen in Fig. 2.9-2.12, the discrepancy in the NEE, ER and GPP fluxes between the two water table depths only occurred in the last week or two of the experiment. What I can infer from this is that throughout most weeks the radish plants were equally efficient at removing atmospheric CO_2 in the -30 cm treatment as in the -50 cm treatment. However, during the ultimate growth stage the radish roots expanded down the core profile and the root growth limitation imposed by the water table in the -30 cm treatment became obvious. Consequently, nutrient absorption was negatively affected, which reduced the accumulation of biomass and the CO_2 uptake of each individual plant.

2.4.6 Comparison between the current study and the data collected by Musarika et al. (2017)

In the study of Musarika et al. (2017), the water table position had no effect on the dry leaf biomass of radish, however, the dry bulb yield was higher in the -30 cm treatment. This indicates that the greater water availability in peat promoted the sink strength of bulbs. In my experiment, on the other hand, both the aboveground and the belowground biomass were negatively affected by the -30 cm water table, with no changes to biomass partitioning between different sinks. The methodological background may provide an explanation for the stark differences in yield outcomes between the two experiments. The simulated flooding might have been the crucial factor in contributing to the discrepancy in outcomes between my experiment and the one conducted by Musarika et al. (2017). If redox conditions in peat lingered after the cores were drained, toxic products of anoxia might have accumulated and affected the radish growth. The accumulation would be more pronounced in the -30 cm water table treatment as compared to the -50 cm treatment due to the greater effect of capillary rise. Additionally, the flooding might have contributed to nutrient depletion by leaching: as the rooting zone was shallower, the radish plants grown in the -30 cm cores could not absorb as much nutrients as the ones from the -50 cm treatment. Consequently, the poor growth of radish at the -30 cm water table depth in my study, as opposed to the findings of Musarika et al. (2017), might have been a result of difference in soil properties. If the assumption that the flooding was the cause of the contradictory outcomes between this experiment and the one conducted by Musarika et al. (2017) is correct, it would mean that whether a water table of -30 cm produces better, worse or the same radish yields as the field water table would very much depend on the time of the year and drainage practices undertaken before planting. In early spring, low air temperatures in the East of England slow the rate of evapotranspiration, contributing to high water retention in peat. For this reason, planting radish later in the season may be a better option. The link between the products of anoxia and the lower radish biomass in eCO_2 as compared to the ambient treatment is less clear. As described above, the conditions of eCO_2 might have lowered plant transpiration, therefore contributing to the higher soil water content, which led to prevalence of the toxic products of anaerobiosis in peat and a lower uptake of essential nutrients. It is also possible that the eCO_2 conditions affected physiology of radish, and such changes made the crop less economical in nutrient use or diminished the effectiveness of nutrient absorption. One such way of lessening uptake of nutrients would be through morphological alterations of the rooting system, such as reduction in fine root production. More controlled research needs to be done in the area of effects of CO_2 enrichment on crop growth in different types of soil and under different temperature and soil water content conditions.

In both experiments Rh was higher in the -50 cm treatment when compared to the -30 cm treatment. The influence of increasing the water table on CH_4 was similar between the two experiments, however, whereas Musarika et al. (2017) found the oxidation rate of CH_4 to be lower in the -30 cm treatment, with the CH_4 average emissions being mostly negative, my experiment showed the CH_4 fluxes to be primarily positive in the higher water table. This indicates that the simulated flooding had a lingering effect on soil water content, and possibly affected the abundance and composition of methanogenic and methanotrophic microorganisms. Both experiments showed no effect of cropping alone on the CH_4 emissions. Additionally, both studies displayed the same pattern of interaction between the water table level and the plant presence, namely the combination of -30 cm and planting resulted in the highest CH_4 flux (mine) or the lowest CH_4 uptake (Musarika et al., 2017). In both experiments root exudation might have increased methanogenic activity when the water table was high. Radish plants absorbed more CO_2 in the eCO_2 treatment in the experiment of Musarika et al. (2017), but not in my study. Moreover, in experiment of Musarika et al. (2017) the NEE flux was higher in the -30 cm treatment, whereas my results showed no difference in the NEE between the two water table treatments.

2.5 Conclusion

This study demonstrated that increasing the water table from -50 cm to -30 cm has the potential to limit peat degradation and emissions of CO_2, however, at the expense of the yield of radish. A rise in global atmospheric CO_2 concentration would reduce the radish yield, nevertheless, it would not limit C fixation by the crop. The absence of difference in NEE and GPP between the aCO_2 and eCO_2 treatments is reassuring as it shows that in the future climate radish canopies would still absorb as much CO_2, despite the sub-optimal rates of leaf growth. The poor performance of radish under CO_2 fertilisation is difficult to explain, although it might be related to limited nutrient uptake and phytotoxin presence in previously waterlogged peat. The effects I observed in the crop (chlorosis and leaf reddening as well as reduced total biomass) seem to suggest that either nutrient uptake or allocation within the plant tissues was not optimal as a result of CO_2 fertilisation, possibly as a consequence of reduction in the rate of mass flow. Despite the vastness of studies documenting effects of CO_2 fertilisation on plant growth, it seems that there is still much to be learned from reactions of individual crops to the rising atmospheric

CO_2 level. How crops react to CO_2 enrichment under various environmental stresses, especially when grown in different substrates, is an area warranting future exploration.

Chapter 3

Impact of fertilizer, water table, and warming on celery yield and CO_2 and CH_4 emissions from fenland agricultural peat

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Impact of fertilizer, water table, and warming on celery yield and CO_2 and CH_4 emissions from fenland agricultural peat.

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Abstract

Peatlands are globally important areas for carbon preservation; although covering only 3% of global land area, they store 30% of total soil carbon. Lowland peat soils can also be very productive for agriculture, but their cultivation requires drainage as most crops are intolerant of root-zone anoxia. This leads to the creation of oxic conditions in which organic matter becomes vulnerable to mineralisation. Given the demand for high quality agricultural land, 40% of the UK's peatlands have been drained for agricultural use.

In this study we present the outcomes of a controlled environment experiment conducted on agricultural fen peat to examine possible trade-offs between celery growth (an economically important crop on the agricultural peatlands of eastern England) and emissions of greenhouse gases (carbon dioxide (CO_2) and methane (CH_4)) at different temperatures (ambient and ambient + 5°C), water table levels (-30 cm, and -50 cm below the surface), and fertilizer use.

Raising the water table from -50 cm to -30 cm depressed yields of celery, and at the same time decreased the entire ecosystem CO_2 loss by 31%. A 5°C temperature increase enhanced ecosystem emissions of CO_2 by 25% and increased celery dry shoot weight by 23% while not affecting the shoot fresh weight. Fertilizer addition increased both celery yields and soil respiration by 22%. Methane emissions were generally very low and not significantly different from zero.

Our results suggest that increasing the water table can lower emissions of greenhouse gases and reduce the rate of peat wastage, but reduces the productivity of celery. If possible, the water table should be raised to -30 cm before and after cultivation, and only decreased during the growing season, as this would reduce the overall greenhouse gas emissions and peat loss, potentially not affecting the production of vegetable crops.

Keywords: agriculture, peatland, carbon loss, land use change, mitigation

3.1 Introduction

Peatlands cover only 3% of the world's land area, but store 30% of total soil carbon (Global Environmental Centre, 2008). At the same time, peat soils are widely utilised in agriculture: in Europe 14% of the peatland area is under cultivation (Global Environmental Centre, 2008), whilst in the UK, 40% of peatlands have been drained for agricultural use (Dixon et al., 2014) and 24% of the deep peat area in England is being farmed (Natural England, 2010). One of the most important regions for crop production on lowland peats in the UK is the East Anglian Fenlands (the Fens): an area of approximately 3800 km^2 of drained peat in England covering parts of Cambridgeshire, Norfolk, West Suffolk and Lincolnshire (Darby, 1956) (Fig. 3.1). Of this Fenland area, 88% is cultivated, sustaining around 4000 farms and supplying 37% of total vegetable production in England (NFU, 2019). An estimated 89% of the Fens are classified as either Grade 1 or 2 agricultural land: the best scores on a five grade scale, which describes suitability for cultivation in England and Wales, where more valuable crops with higher nutritional and water demands such as vegetables are cultivated (NFU, 2019). The fenland soils are especially fertile and account for nearly half of the Grade 1 agricultural land in England. Cultivation of peat soil requires drainage as most crops are intolerant of root-zone anoxia. This leads to the creation of oxic conditions in the upper part of the peat column, resulting in increased vulnerability of the organic matter to mineralisation by aerobic microorganisms and therefore peat wastage (Global Environmental Centre, 2008). It is estimated that Fenland peats store 41 Tg of carbon, which is being lost from the ecosystem at a rate of 0.4 Tg C yr^{-1} (Holman and Kechavarzi, 2011). The drainage-induced volume loss of the peat layer via shrinkage results in soil compaction and oxidation, which cause wastage of thick peat (> 1m) at a rate of about 2.1 cm yr^{-1} and of thin peat (< 1m) at a rate of 1.3 cm yr^{-1} (Holman and Kechavarzi, 2011). This rate of loss means that most of this important area for UK vegetable production will have less than 100 years of cultivation left before the peat is depleted with potential substantial impact on food security.

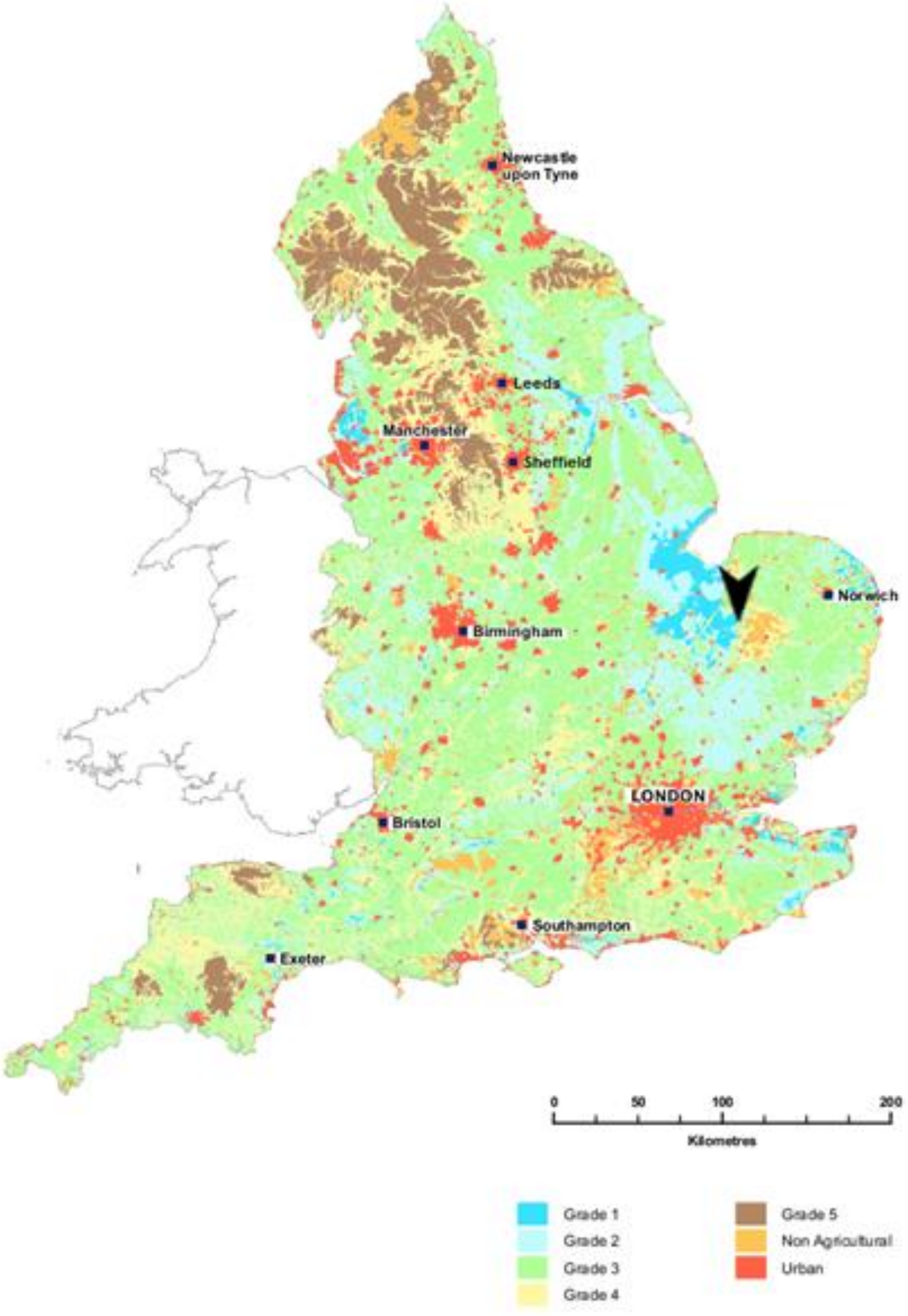

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Figure 3.1: Map of agricultural land in England (the legend indicates the different grades, with 1 indicating the most fertile areas, which are concentrated in the fenland peats south of The Wash, and 5 the lower quality agricultural soils). The black arrow indicates the location where the cores

for the laboratory experiment were sampled (Rosedene Farm in Methwold Hythe, Norfolk in April 2015). Non Agricultural denotes other soil uses, such as landfills, airports, golf courses etc. Source: Natural England, 2010

Shrinkage, compaction and oxidation could be reduced by raising the water table; this has the potential to extend the lifespan of the fertile soil of the Fens. Furthermore, since large areas of the Fens have already sunk below sea level, maintaining drainage requires expensive pumping of water and thus the Fens are increasingly threatened by sea level rise. It is, therefore, crucial to explore the possibility of using a water table level that minimises current peat loss and reduces the need to pump water, while at the same time maintaining economically viable crop growth.

Although the position of the water table is often credited with being of key importance in determining the rate of mineralisation of organic matter, there is insufficient information to guide farmers and farm managers as to the optimal water table position for each specific crop: the majority of studies focus on examining the yield of cereals under different drainage scenarios – for example, wheat (Xu et al., 2013), and maize (Florio et al., 2014). Very little work has been published on the performance of horticultural field crops grown under varying water table levels, with studies offering conflicting results (Dodds et al., 1997; Stanley and Harbaugh, 2002; Musarika et al., 2017).

Mineralization of organic matter also affects the climate by increasing the emission of greenhouse gases (GHG) such as CO_2 and CH_4. The majority of studies on the impact of the water table on GHG emissions in temperate and northern peatlands demonstrate that a rise in the position of the water table decreases emissions of CO_2 while increasing release of CH_4 (Nykanen et al., 1995, Dinsmore et al., 2009, Wilson et al., 2016, Karki et al., 2016 Strack et al., 2004, Hou et al., 2013, Poyda et al., 2016, Regina et al., 2015, Yrjälä et al., 2011). However, in several studies no link has been found between the water table level and GHG emissions (Regina et al., 2007, Lafleur et al., 2005; Schrier-Uijl et al., 2010, Muhr et al., 2016; Dirks et al., 2000). Despite the importance of preserving agricultural peats and reducing GHG emissions, there is a lack of studies testing more sustainable water table levels which could both maintain current crop yield and minimise GHG emissions (Regina et al., 2015; Taft et al., 2017; Taft et al., 2018). While a deeper water table (-40 to -50 cm) could maximize yield, a shallower water table (e.g. -30 cm) might be able to maintain 90% of the productivity whilst reducing peat mineralisation by 30-40% (Renger et al., 2002) thereby substantially extending the future potential numbers of years of cropping before complete peat wastage.

The carbon loss from the Fens can also be stimulated by increases in temperature. The average global temperature increase expected for this region is expected to be within the range of 0.3-4.8°C by the end of this century (relative to 1986-2005) (IPCC, 2014). It is estimated that under the highest greenhouse gas emission scenario, temperatures in Eastern England would rise by 1.4°C to 5.7°C in winter and by 1.3°C to 7.5°C in summer by 2080 (IPCC, 2014). Rising temperatures are predicted to accelerate the rate of organic matter mineralisation, which will lead to higher emissions of greenhouse gases as well as increased plant growth due to enhanced availability of nutrients which are released during mineralisation (Rustad et al., 2001). The effects of higher temperatures on both crop growth and GHG emissions are still highly uncertain.

To address these critical issues discussed above, in this study we explored the impacts of water table, fertilization and warming, on mineralisation of Fen peat, the yield of celery as well as the emissions of CO_2 and CH_4, and the carbon leaching out of the system as dissolved organic carbon (DOC). We hypothesise that increasing the water table from a field depth of -50 cm to -30 cm would not affect celery yield, would decrease emission of CO_2 while only slightly increasing CH_4 flux, and would increase DOC concentration in drainage water. We expect that increasing the temperature (by 5°C) would increase celery yield and increase DOC in the soil water, raise CO_2

respiration but only slightly affect CH_4 emission. Finally, we hypothesize that fertilization would increase celery yield, increase GHG emissions and increase DOC loss.

3.2 Methodology

3.2.1 Sample area and soil collection

Peat cores were sampled from a typical fen peatland at Rosedene Farm in Methwold Hythe, Norfolk, that has been drained after World War II, intensively cultivated, fertilized and used to grow vegetables including celery. The crops are rotated each year, most common crops includes celery, lettuce, Chinese leaf, bulb onions, potatoes, red beet, radish, carrots, and leeks. Although we sampled from a single field, these flat peatlands are highly homogeneous, having undergone the same oxidative processes to the same depths, as the water tables are fixed to standard depths over large areas, and similar high-value crops are widely grown on these soils. The historical studies of Methwold peat close to the sampled field in our study have shown that across 12 sites more than 20 years of intensive agriculture on drained peat has led to homogenization of the top 50 cm into uniformly amorphous humified peat irrespective of earlier differences in the peat which ranged from semi-fibrous to fibrous in the early 1980's (Dawson et al., 2010). The sampling site is within 1-2 km of a flux tower measuring CO_2 fluxes from these agricultural peatlands at Methwold (Morrison et al., 2013). Rainfall in the Fens is below 600 mm a year and the soil of the area is predominately peat, which can be as deep as 2-3 m (Evans et al., 2016). The C:N ratios for the site are presented in Evans et al., (2016), and are low (15:1) due to management practices such as nitrogen fertilizer additions. Moreover, bulk density varied with location and depth depending on the time of year. In particular the surface bulk density was measured to range from 0.3 – 0.5 g cm^{-3} and with depth (0-1 m) between 0.3 – 0.7 g cm^{-3} (Evans et al., 2016).

In the typical field at Rosedene Farm selected for sampling, the farmer maintains the water table position at about -50 cm for crop production, mainly as a higher water table might affect the use of machinery on site (Martin Hammond, pers. comm.). A total of 64 peat cores with a diameter of 11 cm were randomly sampled to a depth 60 cm from across the field in April 2015 (Fig. 3.1), using a sampling design reported in Musarika et al. (2017).

The soil core collection was performed using PVC pipes, which were inserted into the soil. The PVC pipes were excavated out of the ground, preserving the existing soil structure of intact cores within the pipes. The pipes were capped at the bottom to retain the field soil moisture.

3.2.2 Treatment design

We tested the hypotheses in a multifactorial experiment that varied the water table (two levels -30 cm, and -50 cm below the surface), the air temperature (ambient and ambient + 5°C), and two fertilization levels (liquid fertilizer -see details below, and without any fertilisation) on peat cores incubated in controlled environment chambers for a simulated growing season. Celery was chosen as the study species as it is one of the most profitable crops according to the farmer (Martin Hammond, pers. comm.), and it is a marshland plant and therefore should be well-adapted to conditions of an elevated water table (Seale, 1975). Celery was planted in half of the 64 cores collected from the field, while the other half of the cores were left unplanted. The full combination of experimental factors (water table, air temperature, fertilizer and crop) were replicated four times as shown in Fig. 3.2.

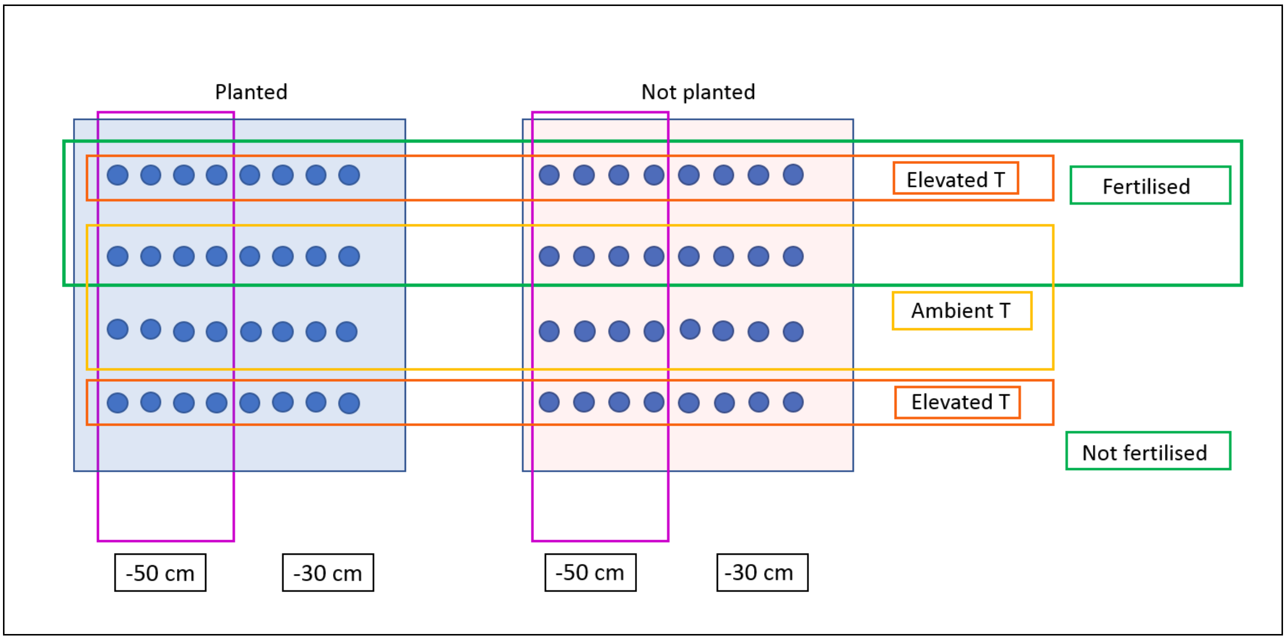

Figure 3.2: Multifactorial experimental design comprising two temperature treatments (ambient and ambient + 5°C), two planting treatments (planted with celery, not planted), two water table treatments (-30 and -50 cm below the surface) and two fertilisation treatments (fertilised and not fertilised).

The two water table levels represent the current conditions in the field (-50 cm) and the level (-30 cm) which has been proposed to reduced greenhouse gas emissions and retain productivity of a grassland (Renger et al., 2002), and radish (Musarika et al., 2017). The water table in each core was monitored with the use of 20 mm diameter drainage pipes with holes every 1 cm wrapped in fine nylon mesh to prevent clogging of the holes with soil. The water table was measured once a day in the drainage pipe with a marked stick and distilled water was added in the pipe if necessary to maintain the water table at the set level. Towards the end of the experiment, the water table was measured and adjusted twice a day to compensate for higher evaporation which resulted from the elevated temperatures.

In order to regulate temperature conditions, the cores were placed in two CONVIRON BDW 40 growth chambers (CONVIRON Controlled Environments Ltd., Winnipeg, Manitoba, Canada). Inside the chambers the air temperature was regulated in real time with an accuracy of ± 0.5 °C.

The ambient temperature was set to the weekly average daytime temperature collected from a meteorological station in the field over a three year period (2013-2015, Cumming et al. unpublished data). This resulted in an ambient temperature equal to 17 °C at the beginning of the experiment, which was then raised to 18 °C in week 4, to 19 °C in week 5, and to 20 °C from week 6 until the end of the experiment reflecting the field conditions in June, July and August. The elevated temperatures followed this same pattern – i.e. commencing at 22 °C and rising to 25 °C. The elevated temperature of + 5 °C was chosen as it represents IPCC's most extreme global warming scenario: RCP 8.5, which predicts a global temperature rise of 4.8 °C by the end of this century (IPCC, 2014).

The fertilised cores were treated with the same fertiliser that is used by the farmer on the celery crop: liquid CHAFER 6-6-12 ($[NH_4PO_3]n$ - ammonium polyphosphate), which has the following composition: N – 6% w/v, K_2O – 12% w/v, and P_2O_5 – 6% w/v. It was applied at the same rate that the farmer uses for the celery crop: 800 l ha^{-1}. The fertiliser was dissolved in 25 ml DI water before application by watering of the cores. The PVC pipe used in this experiment has a cross-sectional area of 94.99 cm^2, therefore each core from the fertilised treatment was enriched with 0.8 ml CHAFER 6-6-12, which was diluted in 25 ml distilled water prior to addition.

The air humidity in both chambers was kept constant at 70% and the PAR (Photo-synthetically Active Radiation) varied between 670-740 µmol m^{-2} s^{-1}. Air humidity and PAR settings of this experiment are based on the average June, July and August conditions recorded from the field in years 2013, 2014 and 2015 and are consistent with a previous experiment on radish using soil cores from this site (Musarika et al., 2017). In both chambers the daylight conditions lasted 12 h (12 h for night conditions) throughout the growth period. Soil water content was measured in the top 12 cm every week with a Campbell Scientific CS655 probe.

3.2.3 Crop planting and biomass measurements

The experiment lasted for a total of 14 weeks. In week one pre-germinated three-weeks-old celery seedlings were planted into half of the peat cores. Fertiliser was added only once, one day before planting. In week 14 the celery was harvested and separated into shoots (leaves and stems) and roots. The cores were excavated and the roots were extracted by washing the peat with tap water under a 1 mm sieve (initial separation) and a 600 µm sieve (final separation). Afterwards the root samples were dried at 80°C for 3 days and weighed to a precision of 0.01 g (dry root biomass).

We measured the C/N ratio of the topsoil peat. The peat soil samples were extracted at harvest from a depth of 0-5 cm (topsoil). The samples were dried at 105°C, then ground to fine powder in a ball mill (Fritsch Pulverisette, Germany) and stored in sealed plastic vials. The samples were analysed on a Vario EL Cube, Elementar C/N analyser.

3.2.4 Greenhouse gas fluxes

CO_2 and CH_4 concentrations were measured once a week for 11 weeks using an LGR Ultra Portable Gas Analyser GGA-30p (Los Gatos Research, Mountain View, CA, USA), with a measurement frequency of one hertz (one measurement per second). Two custom-made PVC chambers both with a volume of 2.8 L were used to record fluxes, one transparent for light measurements (e.g. net ecosystem exchange, NEE) and an opaque chamber for dark measurements (indicated as ecosystem respiration, (ER) in the cores with celery presence, and soil respiration (Rh) in the cores with the absence of the crop). The autotrophic respiration was estimated as the difference between 1) the ecosystem respiration in the planted cores, and 2) the ecosystem respiration in the cores where no crops were planted. The chambers were placed on the top of pipes as shown in Fig.3.3. The gross primary production (GPP) was estimated as the sum of ER and NEE. The rates of change in gas concentration in the chambers were used to estimate the CO_2 and CH_4 fluxes as described in McEwing et al. (2015). We also used flux tower data collected at Methwold (Morrison et al., 2013), close to our sampled field, for comparison with chamber GHG measurements. The flux tower data covered 60 days of crop cycle from 22 June to 20 August 2012, and a 60 day fallow period to 19 October 2012 (Morrison et al., 2013).

Figure 3.3: The transparent headspace chamber for gas flux used for the CO_2 and CH_4 concentration measurements from plants and soil under controlled lighting conditions (e.g. Net Ecosystem Exchange).

3.2.5 Dissolved organic carbon (DOC), NH_4^+ and NO_3^- in water samples

Samples for DOC analysis were collected from the bottom of cores at -50 cm into 20 ml vials with a syringe connected to a pipe, filtered through Fisherbrand M300 0.7 µm glass fibre filters within 8 hours of collection and refrigerated at 6 °C in plastic vials. The vials were previously washed in a solution of 10% nitric acid and 10% hydrochloric acid to remove easily-released carbon. Afterwards the samples were analysed on a Sievers 5310C Total Organic Carbon (TOC) Analyser. Potassium hydrogen phthalate TOC calibration standards at concentrations of 1, 5, 10 and 30 mg l^{-1} were run with each batch of samples. Samples were diluted with ultrapure (18 MΩ) deionised water to bring them within the analytical range. The detection limit was 4 µg l^{-1}.

Drainage samples for NH_4^+ and NO_3^- analysis were filtered on 0.45 µm filters within 8 hours of collection and immediately frozen in plastic vials, awaiting analysis. Upon defrosting, the samples were analysed using the colorimetric method (Mulvaney, R.L., 1996; Mackereth et al., 1989) on 7315 UV/Vis spectrophotometer.

3.2.6 Statistical analysis

Statistical analysis was performed using the open source programme R version 3.3.1 (R Development Core Team, 2017). The CH_4, NEE and ecosystem respiration fluxes were log-transformed, to meet the assumptions of linear models, and ANOVA. We used both linear models and linear mixed models as described in the following paragraphs. Linear mixed effects models were used to test the effects of water table level, temperature and fertiliser use on celery biomass and emissions of CO_2 and CH_4 for the entire dataset including weekly measurements, with 'week' and 'core' as random effects, to take into account the temporal and spatial pseudoreplication. Linear models were used on the fluxes averaged over the entire experiment. The linear mixed models and the linear models were then compared to test if the averaging removed some important information. Outliers, as determined by the Cook's distance which affected the CH_4 flux models, were removed. For the linear mixed models analyses we used the lme4 package (Bates, Maechler and Bolker, 2014) and reported $\chi 2$ in the place of the F-value. The linear models were estimated using the "lm" function in R. The DOC values were averaged across weeks. The biomass and DOC data sets were analysed using ANOVA. The adequacy of all models was assessed by visual inspection of residual plots. When mixed effects models were used, the statistical significance of each factor was determined by likelihood ratio tests performed with the Anova () function between the full model and a model that only included the random effects (weeks and cores). The statistical significance levels used were P-value <0.05 and >0.01 (*); P-value < 0.01 and > 0.001 (**), and P-value <0.001 (***).

3.3 Results

The fresh weight of celery shoots was on average 19% lower with the water table at -30 cm compared to the normal depth of -50 cm (Table 3.1; Fig. 3.4a). The same trend was followed by the dry weight of celery shoots (Table 3.1), which were also on average 19% lower in the -30 cm water table treatment (Fig. 3.4b). Celery shoot fresh weight was not significantly affected by temperature (Table 3.1; Fig. 3.4a), while the dry weight was 23% higher in the elevated temperature treatment (Table 3.1; Fig. 3.4b). Fertiliser use increased the shoot fresh weight by 22% (Table 3.1; Fig. 3.4a) and the dry weight by 21% (Table 3.1) (Fig. 3.4b). Root dry weight was 33% lower in the -30 cm water table treatment (Table 3.1) and remained unaffected by temperature (Table 3.1; Fig. 3.4b). Fertilized cores had 18% higher root dry weight than the unfertilized cores (Table 3.1; Fig. 3.4b). There were no statistically significant interactions among any of the treatment factors (temperature, water table level, fertiliser treatment) on shoot and root biomass. The root:shoot dry weight ratio was 18% lower (Table 3.1) in the -30 cm water table treatment and was 24% higher (Table 3.1) in the ambient temperature treatment (Fig.

3.4c). There was no significant effect of fertiliser addition on the root:shoot ratio (Table 3.1; Fig. 3.4c).

	df	F-value	P-value
Root dry weight			
Water table	1, 28	20.63	**<0.001*****
Fertiliser	1, 28	5.07	**0.033 ***
Temperature	1, 28	0.15	0.699
Water table*Temperature	1, 28	0.12	0.736
Water table*Fertiliser	1, 28	0.81	0.377
Fertiliser*Temperature	1, 28	0.5	0.487
Shoot fresh weight			
Water table	1, 28	13.03	**0.001 ****
Fertiliser	1, 28	16.39	**<0.001*****
Temperature	1, 28	1.58	0.22
Water table*Temperature	1, 28	0.6	0.444
Water table*Fertiliser	1, 28	0.09	0.769
Fertiliser*Temperature	1, 28	0.02	0.901
Shoot dry weight			
Water table	1, 28	11.41	**0.002 ****
Fertiliser	1, 28	14.94	**<0.001*****
Temperature	1, 28	18.22	**<0.001*****
Water table*Temperature	1, 28	0.19	0.67
Water table*Fertiliser	1, 28	0.16	0.694
Fertiliser*Temperature	1, 28	0.0	0.956
Root:Shoot dry weight ratio			
Water table	1, 24	16.03	**<0.001*****
Fertiliser	1, 24	0.11	0.74
Temperature	1, 24	19.15	**<0.001*****
Water table*Temperature	1, 24	0.0	0.991
Water table*Fertiliser	1, 24	2.25	0.147
Fertiliser*Temperature	1, 24	0.83	0.372

Table 3.1: Effects of environmental variables and their interactions on biomass using linear models applied to the biomass values collected at the end of the experiment. The statistical significance levels used were: * = P< 0.05 and >0.01; ** = P< 0.01 and > 0.001; and *** P< 0.001; df = degrees of freedom.

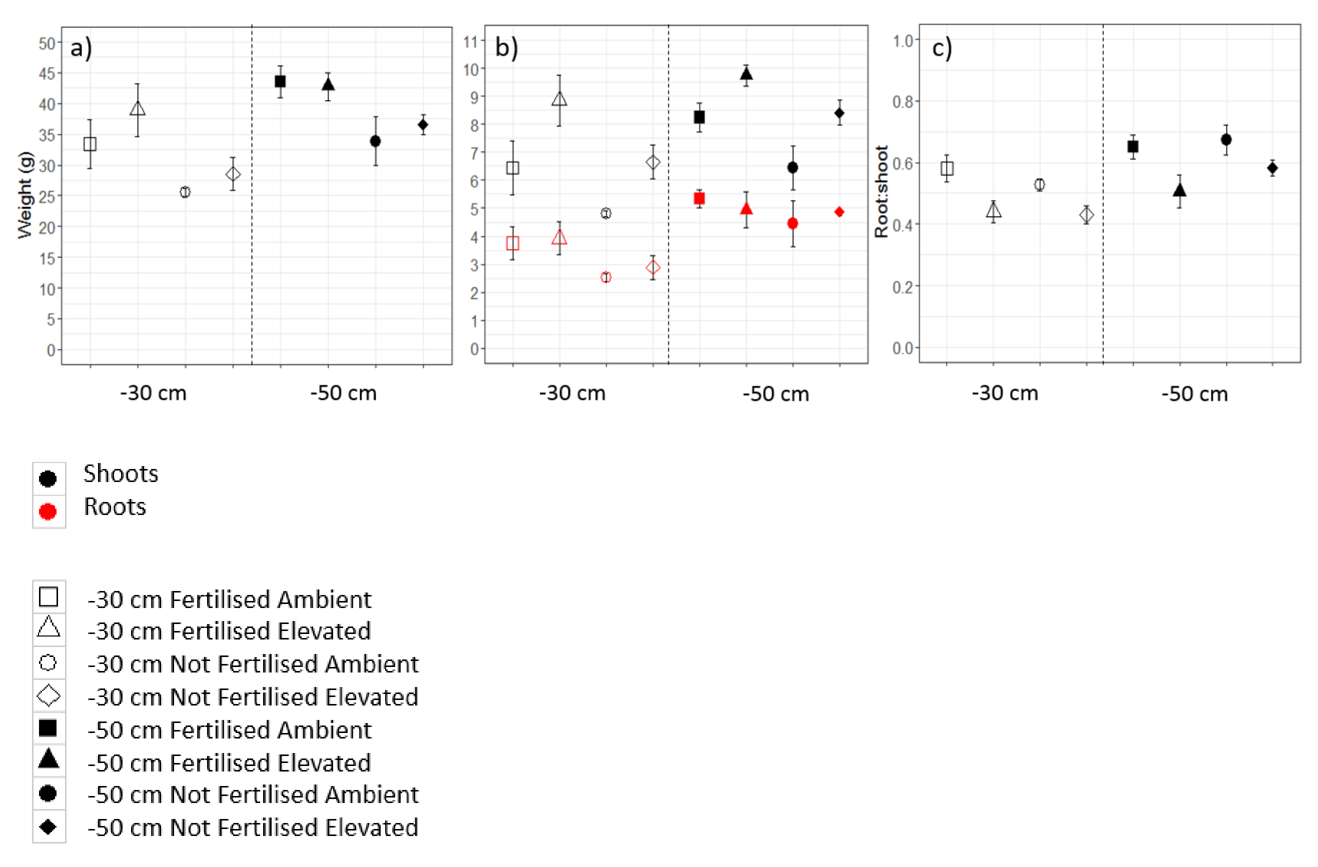

Figure 3.4: Biomass of shoots (leaves and stems, in black) and Roots (in red): a) when fresh, and b) oven dried, and c) dry root:shoot dry weight ratio sampled at the end of the experiment. The water table was kept at either -30 cm or -50 cm (as indicated in the x-axis), and air temperatures at ambient or ambient +5°C, and half the peat cores received fertilizer. Displayed values are means and standard errors (n=4).

Soil respiration (Rh) was 25% higher in the elevated temperature treatment (Table 3.2) than in the ambient conditions and also 31% higher in the -50 cm water table treatment (Table 3.2; Fig. 3.5a) than with a -30 cm water table. The Rh was 22% higher in the fertilised cores as compared with those not fertilised (Table 3.2; Fig. 3.5a).

	linear model			**linear mixed model**		
CH_4 flux	**df**	**F-value**	**P-value**	**df**	**χ2**	**P-value**
Water table	1, 48	0.03	0.862	1	0.87	0.35
Fertiliser	1, 48	1.92	0.172	1	0.75	0.386
Temperature	1, 48	14.07	**<0.001*** **	1	1.26	0.262
Crop presence	1, 48	9.44	**0.003 ****	1	4.13	**0.042 ***
Moisture	1, 62	1.77	0.188	1	1.25	0.263
Water table*Fertiliser	1, 48	0.84	0.363	1	0.58	0.447
Fertiliser*Temperature	1, 48	0.37	0.545	1	0.4	0.528
Water table*Temperature	1, 48	11.87	**0.001 ****	1	4.5	**0.034 ***
Crop presence *Water table	1, 48	6.52	**0.014 ***	1	0.3	0.583
Crop presence *Fertiliser	1, 48	0.01	0.917	1	0.06	0.807
Crop presence *Temperature	1, 48	3.68	0.061	1	0.35	0.552
Water table*Fertiliser*Temperature	1, 48	0.85	0.36	1	0.0	0.973
Water table*Fertiliser* Crop presence	1, 48	0.09	0.77	1	4.99	**0.025 ***
Water table*Temperature* Crop presence	1, 48	13.84	**<0.001*** **	1	4.88	**0.027 ***
Fertiliser*Temperature* Crop presence	1, 48	0.02	0.895	1	0.36	0.546
NEE						
Water table	1, 24	0.09	0.761	1	2.09	0.148
Fertiliser	1, 24	1.35	0.257	1	1.02	0.311
Temperature	1, 24	2.88	0.103	1	0.01	0.93
Water table*Fertiliser	1, 24	0.41	0.53	1	0.8	0.372
Water table*Temperature	1, 24	0.06	0.807	1	0.05	0.828
Fertiliser*Temperature	1, 24	0.81	0.377	1	0.41	0.524
Water table*Fertiliser*Temperature	1, 24	0.48	0.494	1		
GPP						
Water table	1, 24	1.16	0.292	1	0.01	0.937
Fertiliser	1, 24	4.45	**0.045 ***	1	0.32	0.57
Temperature	1, 24	52.16	**<0.001*** **	1	3.01	0.083
Water table*Fertiliser	1, 24	0.07	0.795	1	0.27	0.606
Water table*Temperature	1, 24	0.66	0.423	1	0.04	0.839
Fertiliser*Temperature	1, 24	0.89	0.355	1	0.58	0.448
Water table*Fertiliser*Temperature	1, 24	0	0.968	1	0.03	0.861

Soil respiration (Rh)						
Water table	1, 24	37.85	**<0.001*****	1	9.17	**0.002 ****
Fertiliser	1, 24	3.11	0.091	1	29.49	**<0.001*****
Temperature	1, 24	22.55	**<0.001*****	1	6.69	**0.0097 ****
Water table*Fertiliser	1, 24	0.09	0.766	1	1.78	0.182
Water table*Temperature	1, 24	7.93	**0.0096 ****	1	0.62	0.432
Fertiliser*Temperature	1, 24	3.74	0.065	1	2.9	0.088
Water table*Fertiliser*Temperature	1, 24	0.8	0.379	1	2.32	0.128
Ecosystem respiration (ER)						
Water table	1, 24	0.98	0.333	1	2.79	0.095
Fertiliser	1, 24	1.8	0.192	1	1.15	0.283
Temperature	1, 24	35.99	**<0.001*****	1	24.41	**<0.001*****
Water table*Fertiliser	1, 24	0.09	0.764	1	0.75	0.386
Water table*Temperature	1, 24	0.48	0.495	1	1.06	0.304
Fertiliser*Temperature	1, 24	0.12	0.727	1	0.36	0.546
Water table*Fertiliser*Temperature	1, 24	0.31	0.581	1	0.81	0.368

Table 3.2: Effects of environmental variables and their interactions on gas fluxes from peat cores using both the linear mixed model (which included ‘week’ and ‘core’ as random effects, to take into account the temporal and spatial pseudoreplication) and linear models (which were applied to the fluxes averaged over the entire experiment). The statistical significance levels used were: * = P <0.05 and >0.01; ** = P < 0.01 and > 0.001; and *** P <0.001; df = degrees of freedom.

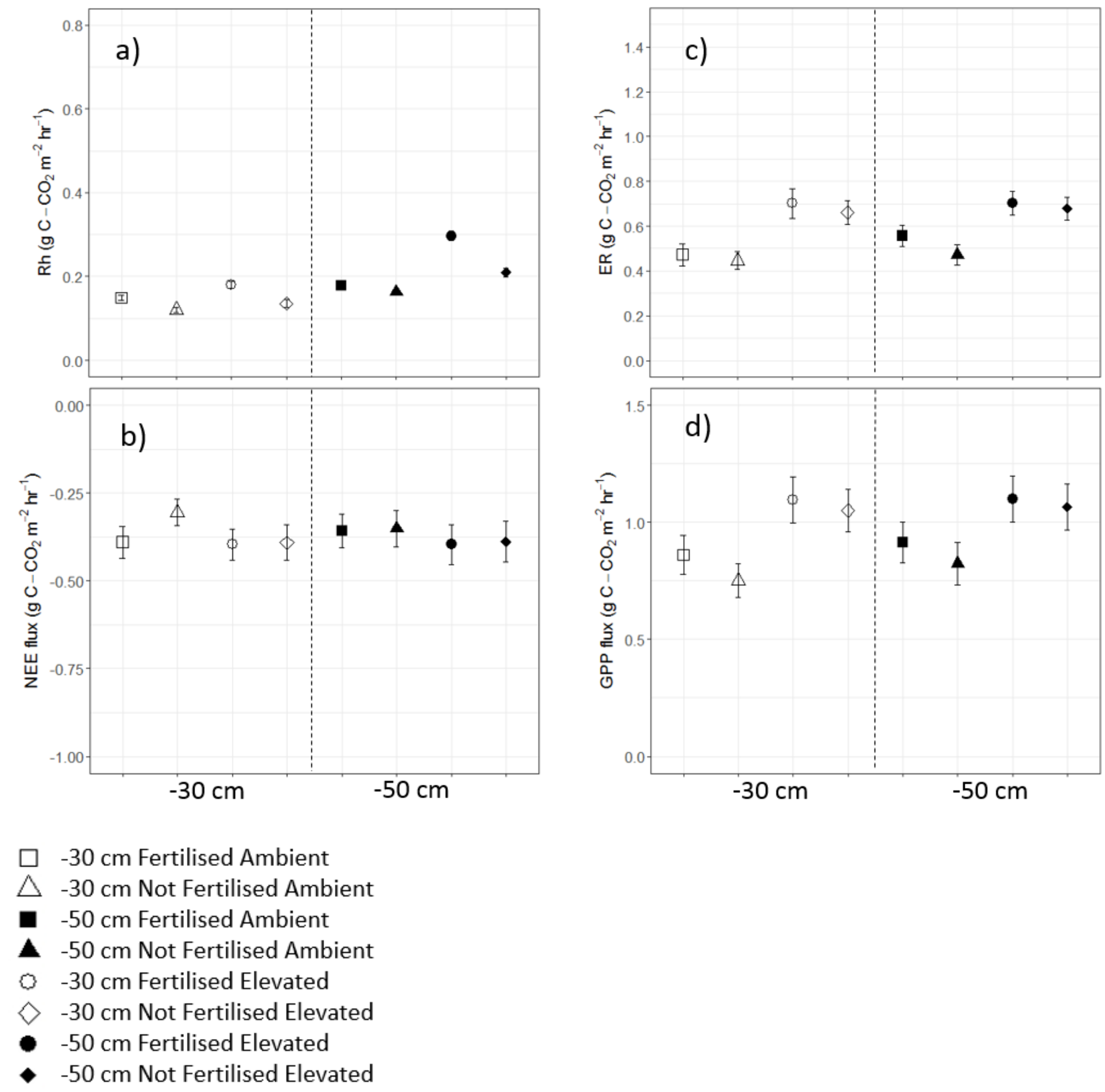

Figure 3.5: Mean respiration averaged over 11 weeks for: a) soil (Rh); b) NEE; c) ecosystem respiration (ER) together with d) GPP over the same time period. In each case the water table was kept at -30 cm or -50 cm, and air temperatures at ambient or ambient +5°C, and half the peat cores received fertilizer. Displayed values are means and standard errors (n=4).

Ecosystem respiration (ER) was also affected by temperature, being higher in the elevated temperature treatment (Table 3.2; Fig. 3.5c), but there were no significant differences in ER between the two water table levels and the fertiliser treatments (Table 3.2; Fig. 3.5c).

Gross Primary Production (GPP) was greatest in cores under elevated temperature (Table 3.2), while water table depth and fertiliser addition did not appear to have a significant influence on these values (Table 3.2; Fig. 3.5d). None of the interactions among factors was significant for GPP. Net Ecosystem Exchange was not significantly affected by any of the factors (Table 3.2).

While the statistical results were fairly consistent for NEE, RE or Rh and GPP, there was a difference in the outcomes between the two statistical approaches employed for the CH_4 fluxes (Table 3.2). The linear model (Table 3.2, left columns) showed that the water table and fertiliser treatments had no effect on the CH_4 flux, however, the presence of the crops and temperature showed significant effects on CH_4 fluxes (Table 3.2; Fig. 3.6). In the linear mixed model (Table 3.2, right columns) CH_4 fluxes were unaffected by temperature, water table, and fertiliser use, however, there was an effect of the presence of the crops. Based on the linear model, the elevated temperature resulted in more than doubling in the averaged emissions compared to ambient conditions, and a shift from CH_4 consumption to CH_4 loss into the atmosphere. On average, planted cores had more than twice the rate of CH_4 emissions when compared to the unplanted cores, but the planted cores with a -50 cm water table showed both CH_4 consumption and emission. Soil moisture did not influence CH_4 flux in either the linear model (Table 3.2, left columns) or the linear mixed model (Table 3.2, right columns).

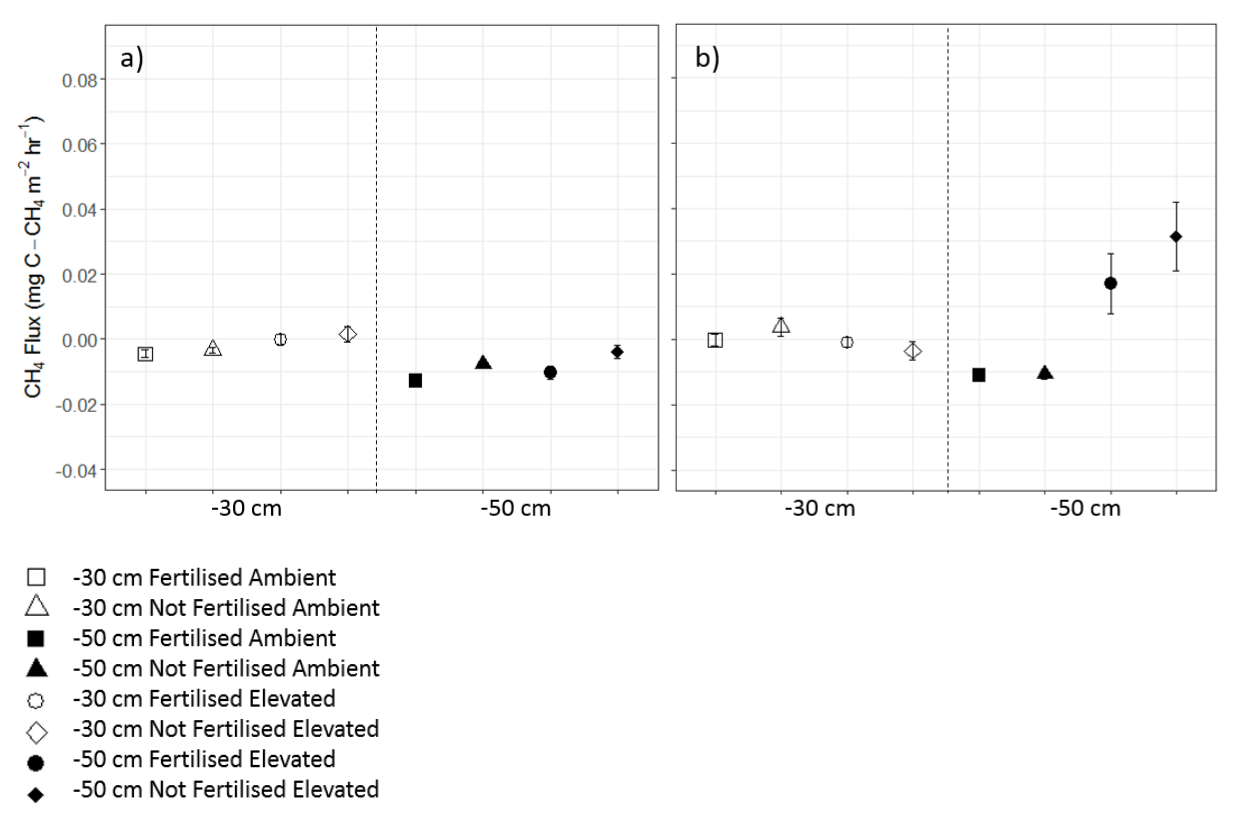

Figure 3.6: Average CH_4 flux over a period of 11 weeks from: a) not planted; b) planted cores, with water table kept at -30 cm or -50 cm and with ambient air temperatures or +5°C air temperature, in cores with and without fertilizer additions. Displayed values are means ± SE (n=4).

Drainage DOC concentrations were 45% higher in the elevated temperature treatment, and 22% higher in the -30 cm water table treatment (these differences were statistically significant, Table 3.3). DOC concentrations were 40% lower in cores with crop presence and were not affected by fertiliser addition (Table 3.3, Fig. 3.7). There was a statistically significant interaction between water table and crop presence on DOC concentration (Table 3.3). Soil water content was significantly affected by the presence of the crops and water table level, but there was no effect of temperature (Table 3.3).

Soil water content	**df**	**χ2**	**P-value**
Crop presence	1	15.71	**<0.001*** **
Water table	1	57.77	**<0.001*** **
Temperature	1	0.08	0.772
DOC	**df**	**F-value**	**P-value**
Water table	1, 48	8.58	**0.005 ** **
Fertiliser	1, 48	0	0.98
Temperature	1, 48	28.13	**<0.001*** **
Crop presence	1, 48	51.8	**<0.001*** **
Water table*Fertiliser	1, 48	0.85	0.362
Water table*Temperature	1, 48	1.96	0.168
Fertiliser*Temperature	1, 48	0.15	0.697
Water table* Crop presence	1, 48	11.06	**0.002 ** **
Fertiliser* Crop presence	1, 48	0.36	0.553
Temperature* Crop presence	1, 48	3.62	0.063
Water table*Fertiliser*Temperature	1, 48	1.52	0.224
Water table*Fertiliser* Crop presence	1, 48	1.19	0.28
Water table*Temperature* Crop presence	1, 48	3.58	0.065
Fertiliser*Temperature* Crop presence	1, 48	1.58	0.215

Table 3.3: Dependence of soil water content and drainage DOC on environmental variables and their interactions using linear models applied to the moisture and DOC values averaged over the entire experiment. Water table and temperature are categorical variables. The statistical significance levels used were: * = P <0.05 and >0.01; ** = P < 0.01 and > 0.001; and *** P <0.001; df = degrees of freedom.

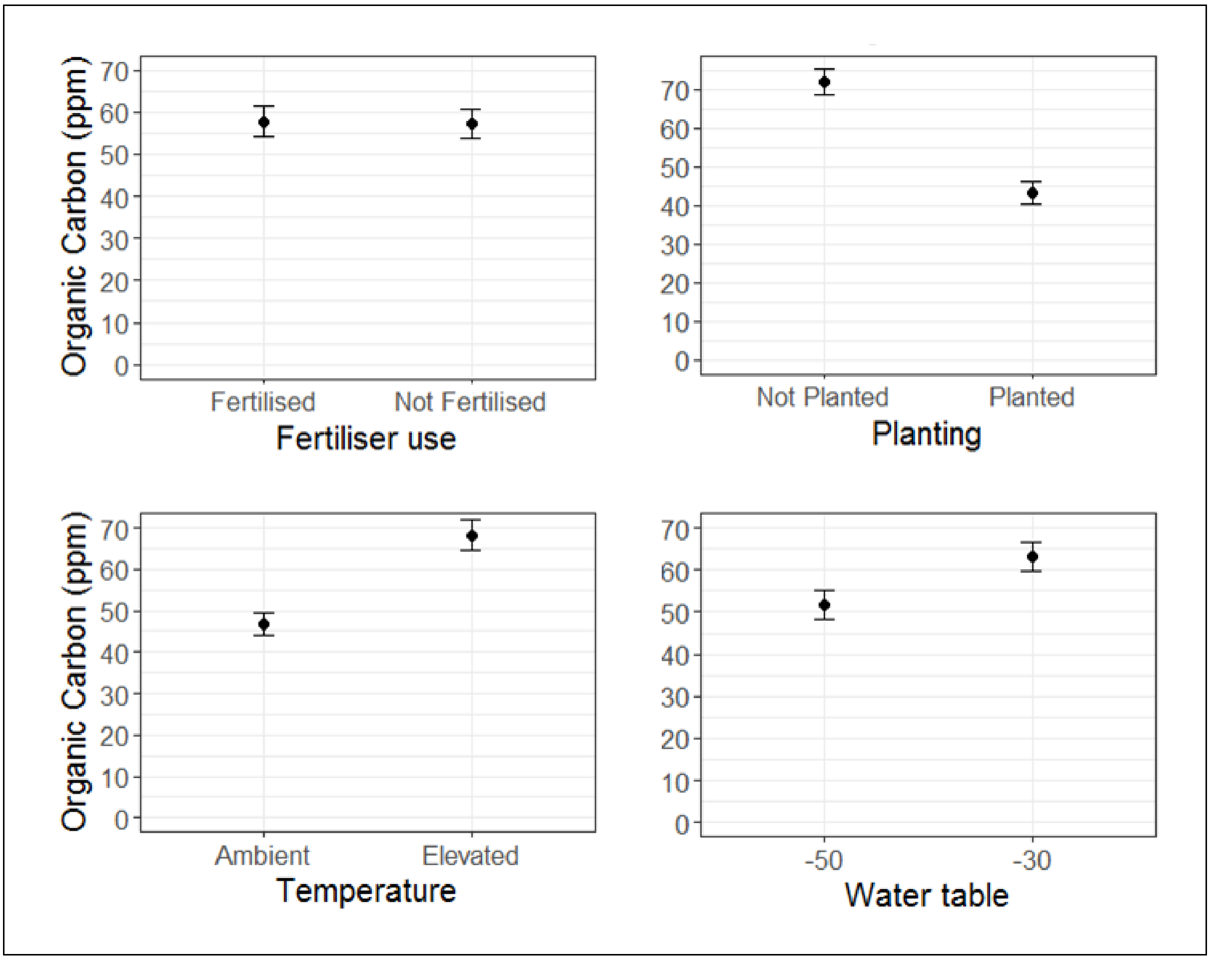

Figure 3.7: Mean (±SE) drainage DOC concentrations in fertiliser (fertilised and not fertilised), planting (cropped and fallow), temperature (ambient and ambient + 5°C) and water table (-30 cm and -50 cm) treatments.

The values of NO_3^- in the drainage water were significantly (nine times) higher in the -50 cm water table treatment when compared to the -30 cm treatment (Table 3.4). The drainage concentrations of NH_4^+ were significantly (three times) lower in the -50 cm water table than when the water table was -30 cm. The values of NO_3^- and NH_4^+ were significantly lower in the planted cores when compared to the cores with no crop presence (Table 3.4). Warming had no significant effect on the NO_3^- content in the drainage water, however, the NH_4^+ drainage concentrations were significantly higher in the elevated temperature treatment (Table 3.4).

There was no significant difference in the concentrations of NO_3^- and NH_4^+ between the cores that were fertilised and the ones that were not (Table 3.4).

NO_3^- concentration			
	df	**χ2**	**P-value**
Water table	1	7.69	**0.006 ****
Fertiliser	1	0.07	0.797
Temperature	1	1.56	0.211
Crop presence	1	38.63	**<0.001*****
NH_4^+ concentration			
Water table	1	32.39	**<0.001*****
Fertiliser	1	0.05	0.83
Temperature	1	22.43	**<0.001*****
Crop presence	1	13.32	**<0.001*****

Table 3.4: Effects of water table depth (-30 cm and -50 cm), fertiliser use (fertilised and not fertilised), temperature (ambient and ambient +5°C) and crop presence (cropped and fallow) on NO_3^- and NH_4^+ concentrations in drainage water.

The topsoil C/N ratio was significantly higher in the elevated temperature treatment as compared to the ambient conditions (Table 3.5). It was also significantly higher in the planted cores as compared to the unplanted cores. There was no significant difference in the C/N ratio between the two fertilisation and the two water table treatments (Table 3.5). The topsoil peat C/N ratio had a narrow range of between 13-14. Methane and Rh fluxes averaged over all weeks were not related to the peat C/N ratio, however, there was a significant negative relationship between DOC concentration in the drainage water and the topsoil C/N ratio.

C/N ratio (topsoil)	**df**	**F-value**	**P-value**
Water table	1, 59	1.95	0.168
Fertiliser	1, 59	0.44	0.511
Temperature	1, 59	4.82	**0.032 ***
Crop presence	1, 59	76.6	**<0.001*****
CH_4			
C/N ratio (topsoil)	1, 62	3.0052	0.088
Rh			
C/N ratio (topsoil)	1, 30	0.2685	0.6081
DOC			
C/N ratio (topsoil)	1, 62	6.5299	**0.01307 ***

Table 3.5: Effects of treatments on topsoil C/N ratio. Effects of topsoil C/N ratio on CH_4, Rh and DOC.

3.4 Discussion

3.4.1 Celery biomass

A higher water table increases the risk of root waterlogging, which may have a negative impact on yield. In our experiment celery roots extended until they reached the water table and the deeper (-50 cm) water table treatment resulted in greater root expansion, explaining the differences in root weight between the two treatments. This indicates that nutrient limitation might be a possible cause of lower root and aboveground biomass from the -30 cm water table treatment (Oomes et al., 1996), which is also consistent with the observed higher biomass with fertiliser addition in our experiment. Our findings are consistent with those of Dodds et al. (1997) who found reduced tomato fruit biomass when a water table was maintained at -30 cm as compared to -60 cm. In contrast, Musarika et al. (2017), who used a similar design to the present study to observe how raising the water table from -50 to -30 cm affected the yield of radish, found improved growth with the shallower water table. This could be due to a higher tolerance to waterlogged conditions of radish and to its shallower and less dense rooting system, and possibly lower nutrient limitation. Similarly, Stanley and Harbaugh (2002) also found increased biomass of *Caladium* under a shallower water table (i.e. -30 to -45 cm vs -60 cm).

The higher shoot biomass in cores exposed to elevated temperatures and deeper water table shows that celery growth will be favoured by warming temperatures and well-drained soils. The maximum temperature used during this experiment (20 °C and 25 °C) and the result of our study are similar to the temperature treatments (19 °C and 24 °C) used by Heißner et al. (2006) which also showed higher asparagus fresh-biomass in the elevated temperature treatment. It has to be noted, however, that differences in the biomass of crops grown at different temperatures may be affected by plant water limitation due to higher evaporative demand at higher temperatures, rather than being the direct effect of temperature (Carter et al., 2016). For example, Shaw et al. (2014) showed that temperature increases above 29 °C resulted in lower yields of rainfed maize, however, they found no effect on maize biomass when the plants were irrigated, which points to moisture stress as a potential confounding variable in field studies. For this reason, laboratory experiments (such as this one), where conditions can be better controlled, can provide improved estimations of temperature effects on plant properties allowing a separating moisture from other environmental controls. It has been shown that in conditions of unlimited soil water supply, temperature increases result in higher stomatal conductance (Urban et al., 2017; Marchin et al., 2016) and higher carbon assimilation.

Few studies have examined the effects of soil warming on root development in peatlands converted into agriculture. The results of our study are consistent with findings even from very different ecosystems (e.g. arctic tundra), where increased root production with warming was observed in hollows (depressions below the water table), but not in hummocks (raised areas in between hollows) indicating that microtopography and the position of the water table may play an important role in root dynamics in peatlands (Sullivan et al., 2008). Steinaker and Wilson (2008) reported that the production of roots in grassland and forest ecosystems increases with higher soil temperatures. Similarly, to aboveground yield, effects of temperature increases on roots may be confounded by soil moisture changes. In a grassland study Xu et al. (2015) noted that soil water content in the upper soil layers decreased as a result of warming and a greater portion of the rooting system was allocated to deeper soil layers. Generally, a trade-off is expected between production of roots and aboveground biomass as both compete for photosynthates (Radville et al., 2016), and conditions which favour root development could also decrease aboveground crop yield. In this study, the root dry weight was not significantly different between the ambient and the elevated temperature treatments. Our results suggest that water table depth is the dominant control on root development in these systems, and that higher temperatures do not significantly stimulate root biomass when soil water content is maintained as a constant.

3.4.2 Peat C/N ratio

Whether soil C/N ratio could be considered a good predictor of organic matter mineralisaton (and so GHG emissions) is a topic of contestation, with studies showing mixed results. C/N ratio can be a good indicator of the degree of organic matter humification and therefore its potential for GHG release (Marty et al., 2017). Some studies show that mineralisation rates are higher in soils with lower C/N ratios (Gundersen et al., 1998; Ollinger al., 2002; Klemedtsson et al.,, 2005; Zhang and Marschner, 2016). Ostrowska and Porębska (2015) noted that while the C/N ratio was correlated with the rate of organic matter mineralisation, the percentage of DOC in SOC was a better predictor of organic matter decomposition. Šantrůčková et al. (2010) reported that the C/N ratio was only one of several factors (others being bulk density, total soil C content, vegetation type) controlling soil CO_2 emissions. Values of the C/N ratio which are greater than 20 are also found to correspond with reduced rates of decomposition of soil organic matter as immobilisation of N by biotic and abiotic processes may occur (Bengtsson et al., 2003; Springob and Kirchmann, 2003; Zhang and Marschner, 2016). Immobilisation of N in agriculturally-utilised soils would require increased fertiliser inputs in order to achieve a higher yield, however, this phenomenon should not be a problem in the peats of the Fens as the C/N ratio values in our study were below 20.

3.4.3 Ecosystem respiration (ER) and soil respiration (Rh)

The higher Rh from the -50 cm water table treatment indicates that a statistically significant portion of microbial decomposition occurred in the zone between -30 cm and -50 cm. This indicates that the organic matter from the soil layers to a depth of -50 cm are still relatively easy to decompose, and can result in a significant contribution to the overall carbon loss of these ecosystems. Therefore, raising the water table may be a viable option for expanding the lifespan of agricultural peat and possibly the only one as emissions of GHG were reported to be unaffected by practices such as no- and minimum tillage (Taft et al., 2018). Nevertheless, due to negative effects on crop biomass as noted in this study, raising the water table for the duration of the growing season is unlikely to be adopted by farmers. Higher Rh from the elevated (+5°C) temperature treatment indicates increased rates of organic matter oxidation by soil microorganisms. Elevated temperatures can accelerate the decomposition of organic matter by increasing microbial metabolic rate (Ziegler et al., 2013). Such rates have been shown to rise in an exponential manner until 45-50°C before declining (Yiqi and Zhou, 2006). This has profound implications for climate change and lifespan of peat as temperature increases enhance soil CO_2 emission and thus generates a positive feedback mechanism, which results in more atmospheric warming and more peat loss - an effect increasingly seen across large areas of global peatlands.

Unlike Rh, ER was not influenced by the position of the water table. This result is consistent with Lafleur et al. (2005), Dimitrov et al. (2010) and Updegraff et al. (2001); however, others found higher rates of ER to be related to deeper water tables (Juszczak et al., 2013; Riutta et al., 2007; Bubier et al., 2003). In our study we estimated the autotrophic respiration to contribute to about 70% of ER, which is a higher value than reported in Moore et al. (2002) (50%), Frolking et al.

(2002) (50%), Shurpali et al. (2008) (55%), Crow and Wieder (2005) (35 to 57%). Therefore, it is likely that the water table-induced changes in heterotrophic respiration were offset by the effects on plant-derived respiration.

3.4.4 Gross Primary Production (GPP) and Net Ecosystem Exchange (NEE)

The temperature, fertilizer and water level treatments did not affect the NEE of the planted cores, which indicates that any increases in carbon loss from respiration were offset by increased carbon sequestration by the celery plants. This would imply that crops temporarily compensate the carbon losses by peat oxidation. However, once the crops are removed the peat becomes a substantial net carbon source to the atmosphere.

Net ecosystem exchange in disturbed peats might result in either a carbon loss or a carbon storage. Site drainage history and water table level may act as factors in determining NEE, however, this is not always the case. Aslan-Sungur et al. (2016) reported a drained temperate peatland used in agriculture and peat mining as being a strong carbon source, with NEE varying between 244 and 663 g C m^{-2} yr^{-1}. On the other hand, in some cases abandoned temperate peatlands can be a stronger CO_2 sink than natural bogs (e.g. -128 ± 60 g C m^{-2} yr^{-1} as compared to -46 ± 36 g C m^{-2} yr^{-1}) as a result of greater biomass production and GPP in a drained agricultural peatland which became grassland (Wang et al., 2018). In other cases drained peatlands show no difference in carbon uptake after being restored (Järveoja et al., 2016). The flux tower study conducted at Methwold, close to our sampled field, revealed net CO_2 release from the drained agricultural fen peat to be 61.9 ± 12.7 g C m^{-2} for 120 days, covering the cropping season and early autumn post-cropping (Morrison et al., 2013). This flux rate is equivalent to about 0.021 ± 0.00441 g C m^{-2}, similar to the ER measured in our study (Fig. 3.4). In our study, GPP was only stimulated by increased temperature, suggesting that celery growth is temperature limited in this environment. However, given that NEE was not significantly affected by temperature increase (Table 3.3), the rise in carbon uptake from enhanced plant production is nullified by the increased ER.

3.4.5 CH_4 emissions

As CH_4 emissions from agricultural soils are usually much smaller than those of CO_2 (Zona et al., 2013; Maljanen et al., 2007; Karki et al., 2016) an increase in CH_4 release might not negate the benefit of the decreased CO_2 loss with a raised water table.

Differences in the outcomes between the two statistical approaches used for analysing the CH_4 data complicate the interpretation of the results. These results suggest that once the time-series element is removed, the patterns in the flux become more visible, and that temperature is a dominant control on these fluxes (see Table 3.3 for the linear model), consistent with the high temporal variability in the fluxes potentially confounding the statistical results. Emissions of CH_4 are governed by the interplay of two processes: CH_4 production by methanogens (which requires anoxic conditions) and consumption by methanotrophs (which occurs in oxic conditions) (Aerts and Ludwig, 1997). The position of the water table seems to be crucial in determining whether a site becomes a source of $CH_{4.}$ A number of studies demonstrate that in the agricultural soils a water table of -20 cm or lower is enough for complete oxidation of CH_4 by methanotrophs. Regina et al. (2015) only found CH_4 emissions if the water table was shallower than -20 cm, which is consistent with our study where we mostly found CH_4 uptake (except for the planted cores where we detected CH_4 emissions even with -50 cm water table). In a mesocosm experiment on grassland peat, Karki et al. (2016) showed that CH_4 emissions were negligible at water tables of -30 cm and -40 cm and were significantly higher at 0 cm, -10 cm and -20 cm. Nykanen et al. (1995) reported low emissions or uptake of CH_4 from a fen utilised as a grassland whose water table varied between -20 cm and -117 cm. Poyda et al. (2016) reported insignificant CH_4 emissions from cultivated peat soil (grassland and cropland) for mean water table levels of -

25 cm or deeper. Renou-Wilson et al. (2014) noted the lack of CH_4 emissions from a peat utilised as grassland on sites where the water table was below -30 cm.

The absence of a relationship between water table fluctuations and CH_4 emissions is likely due to the fact that deeper water tables have no or negligible effect on topsoil water content once the water table level is deeper than -30 cm (Juszczak et al., 2013). The moisture level in the near surface soil layers is the key factor controlling methanogenic and methanotrophic activity and therefore CH_4 production and consumption (Stiehl-Braun et al., 2011; Tiemeyer et al., 2016).

Although warming increases the activity of both methanogenic and methanotrophic communities, it does not affect the two groups to the same extent: at low temperature (0-10°C) values, the activity of methanogens is reported to be inhibited to a greater extent than that of methanotrophs, however, the optimum temperature for both groups was found to be 25 °C (Dunfield et al., 1993). Increasing CH_4 emissions with rising temperatures (treatments: 5 °C, 10 °C, 15 °C, 20 °C, 25 °C) were found in a mesocosm experiment on peat soil (van Winden et al. (2012). Interactions between water table position and temperature may also occur as the response of CH_4 emissions from peat to temperature increases can depend on the position of the water table (Dinsmore et al., 2009). In the shallow water table treatment (0 to -5 cm) the increase in temperature led to higher CH_4 emissions, whereas in the low water table treatment (-30 to -35 cm) the CH_4 flux decreased with increasing temperature, which is consistent with the CH_4 consumption being stimulated more under drier conditions.

In the present study, there was no difference in the CH_4 flux between the ambient and the elevated (+5 °C) temperature treatments in the linear mixed model. However, the linear model showed that CH_4 emissions were significantly higher in the elevated temperature treatments. The discrepancy in these results might be linked to the high variability in the impact of temperature, which was not consistent throughout the measurement period, increasing the within-groups variability in the data (and decreasing the statistical significance of temperature).

Once the data were averaged, the impact of temperature was lost, while it appeared significant once the data were modelled taking week and core into account.

The presence of celery was associate with higher CH_4 efflux – this was most likely caused by the addition of substrates in the form of decaying roots and root exudates stimulating methanogenic activity (Segers, 1998; Green et al., 2014). The increased CH_4 loss in the presence of plants is also species-dependent as shown by peat mesocosms with *Molinia caerulea* which had higher CH_4 loss than those with *Sphagnum* and may reflect direct transfer of CH_4 from soil through plant tissues and out of stomata (Leroy et al., 2017). However, unlike *M. caerulea* celery does not have aerenchymous tissue which would allow for CH_4 transportation from the root zone to the atmosphere. Despite this, new root material can increase labile carbon compounds in the soil, supporting CH_4 production (Saarnio et al., 2004).

Although the level of the water table by itself did not affect CH_4 fluxes, it did influence the way CH_4 fluxes were influenced by the presence of crops and temperature (e.g. the interaction term between water table level and temperature was significant in the linear model and marginally significant in the linear mixed model, see Table 3.1). The increase in CH_4 fluxes between ambient and elevated temperature conditions is greater in the -50 cm water table, and it is also more pronounced in the planted cores (e.g. the difference in emissions between planted and unplanted cores is the highest at -50 cm).

3.4.6 Dissolved Organic Carbon

Site hydrology strongly influences DOC concentration in peat water. Peatlands subjected to drainage (such as agricultural peats) leach more DOC than undisturbed ones (Frank et al., 2014). Nevertheless, studies on peatland restoration present mixed results of rewetting on the concentration of DOC (Preston et al., 2011; Tiemeyer and Kahle, 2014; Schwalm and Zeitz, 2015).

In this study the DOC concentration in the -30 cm water table treatment was 1.2 times higher than the one in the -50 cm treatment. In peat soil used in agriculture the majority of DOC is estimated to originate close to the surface due to the greater presence of easily decomposable plant residues (Chow et al., 2006). For this reason, the higher DOC concentration in drainage water of the -30 cm cores could be explained not only by higher volume of peat available for leaching, but also leaching through a layer that is richer in organic compounds. Therefore, raising the water table could increase the loss of carbon as DOC, at least in the short period following rewetting.

Rising temperatures are expected to accelerate microbial decomposition of peat and hence the production of DOC (Preston et al., 2011). In a peat incubation study, Moore and Dalva (2001) report a 2.4-fold increase in DOC release following a temperature rise from 4°C to 22°C. In our study, increasing the temperature by 5°C resulted in an almost doubling of DOC concentrations in the drainage water, adding to the higher carbon loss through Rh and ER.

DOC concentration was 1.5 times higher in the unplanted cores than in planted ones. Vegetation can control production of DOC by affecting hydraulic properties of peat and also by excretion of root exudates (Armstrong et al., 2012). Changes between vegetation forms may also play a role as shown by Leroy et al. (2017) in a peat mesocosm experiment. They found the presence of *Molinia caerulea* to have negative effects on DOC content when compared to *Sphagnum*-only plots. Armstrong et al. (2012) report the highest DOC values in *Calluna* dominated peatlands and the lowest in *Sphagnum*. In this study, the presence of celery plants might have also affected DOC concentration indirectly, by reducing peat water content and increasing microbial or wetting-drying cycle release of DOC as moisture content was lower in the planted cores. The interaction between the presence of crops and water table level on DOC could be linked to the water absorption by roots slowing down the leaching of carbon compounds into the drainage water.

3.4.7 Concentrations of NO_3^- and NH_4^+ in the drainage water

In the process of nitrification ammonium (NH_4^+) is oxidised to nitrate (NO_3^-) or nitrite (NO_2^-): this occurs under aerobic conditions. Subsequently, NO_3^- is reduced to nitric oxide (NO), nitrous oxide (N_2O) and dinitrogen (N_2) in the process of denitrification, which happens when anaerobic conditions are present (Bouwman, 1998; Trost et al., 2013). Nitrate concentrations in water of undisturbed, poorly-drained peats are usually miniscule (as aerobic conditions are needed for nitrification) (Adamson et al., 1998; de Ruijter et al., 2007). However, drained peatlands undergo aeration and therefore tend to have high content of NO_3^- in pore water due to accelerated nitrification (Holden et al., 2004). In our study the concentration of NO_3^- in the drainage water decreased substantially with the higher water table, indicating an increased rate of denitrification. This outcome was expected as the -30 cm water table treatment had higher soil water content values as compared with the -50 cm treatment. However, NH_4^+ displayed an opposite trend as its drainage concentrations were higher in the -30 cm water table when compared to the -50 cm treatment. Since nitrification occurs in aerobic conditions, the rate of transformation of NH_4^+ into NO_3^- was probably reduced in the higher water table, thus resulting in the elevated NH_4^+ concentration values. Other studies present mixed results of water table manipulation and rewetting on NH_4^+ and NO_3^- content in peat. Munir et al. (2017) found peat NH_4^+ concentrations in the topsoil to be unaffected by water table depths of between -38 cm and -120 cm and the topsoil NO_3^- content to increase with a falling water table. Rewetting resulted in higher NO_3^- content in peat drainage water and the largest losses of NO_3^- were recorded in the year with the highest rainfall (Tiemeyer and Kahle, 2014). Similarly to our experiment, a shift in the ratio of NH_4^+ to NO_3^- towards higher NH_4^+ presence after rewetting was also found by Lundin et al. (2017) in a study on a former peat extraction site. We did not manage to quantify N_2O emissions from peat in this experiment, however, the dynamics of NH_4^+ and NO_3^-

would suggest that they could be potentially significant in the -30 cm water table, given the magnitude in the reduction of NO_3^- concentration between the two water table treatments.

Our results show that warming had no effect on NO_3^- content in the drainage water, however, NH_4^+ concentrations were higher in the elevated temperature treatment. Other studies showed that rising temperatures increase both the denitrification and the nitrification rate (Rustad et al., 2001; Veraart et al., 2011; Munir et al., 2017). Warming increasing NH_4^+ concentration in the drainage water which we found in our study signifies that the rate of decomposition of organic matter into inorganic N forms (such as NH_4^+) was accelerated. Studies on peats demonstrated that air temperature increases lower than the one used here (5°C) could alter N transformation, for instance Munir et al. (2017) reported an increase in NH_4^+ in boreal peat samples following a 1°C warming. Our results suggest that global warming of 5°C would cause more loss of NH_4^+ to water bodies. Greater presence of inorganic N in peat could enhance crop growth, however, in our experiment, leaf chlorosis occurred and was more pronounced in the elevated temperature treatment, which suggests that celery plants experienced nutrient limitation.

The presence of celery resulted in depletion of NH_4^+ and NO_3^- in the drainage water, however, the loss of NO_3^- was much higher than that of NH_4^+: the concentration of NO_3^- in the unplanted cores was 13 higher than in the planted cores, meanwhile NH_4^+ concentration in the unplanted cores was only twice as high as in the planted cores. Moreover, whereas in the unplanted cores NO_3^- concentration dominated over NH_4^+, the opposite was true in the planted cores. This would suggest that celery preferentially absorbed NO_3^- over NH_4^+. The lack of an effect of fertiliser addition on the concentrations of NO_3^- over NH_4^+ in the drainage water suggests that celery roots were very efficient at absorbing the fertiliser. This would mean that fertiliser addition at prescribed quantities would not result in its leaching into the drainage water, at least under celery cropping in summer.

3.5 Conclusion

Raising the water table from -50 cm to -30 cm on Fenland peats could decrease yields of celery by 19%, which is likely to be challenging for farmers to accept. However, in the absence of crops, a water table of -30 cm would decrease the rate of peat mineralisation to CO_2 by 31% without affecting CH_4 emissions. This presents an alternative solution to decrease peat loss while potentially maintaining crop yield by increasing the water table level outside of the growing periods of crops, which would at least reduce some of the peat loss before or after cultivation. We recommend replicating the study on a larger scale, as the limited growth space of the cores may not fully represent field conditions. Larger scale in-situ water table manipulations should test our findings under commercial farming conditions in order to validate the applicability of our results from laboratory experiments into the more complex field conditions.

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Chapter 4

Optimizing fen peatland water-table depth for romaine lettuce growth to reduce peat wastage under future climate warming

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Optimizing fen peatland water-table depth for romaine lettuce growth to reduce peat wastage under future climate warming.

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Abstract

Peatlands worldwide store 30% of total soil carbon, but 40% of UK peatlands have been drained for agricultural use which has caused serious peat wastage and associated greenhouse gas emissions (CO_2, CH_4). Amongst the most rapidly degrading peatlands are the East Anglian Fenlands (the Fens) a lowland area in the south-east of the UK, which comprises nearly half the Grade 1 agricultural land in England, and currently supplies 37% of English-produced vegetables, together with high-value field-grown salad crops. There is a critical need to make the growing of high value horticultural crops on The Fens more sustainable, since this currently involves expensive drainage by pumping of water resulting in peat shrinkage, oxidation, and erosion causing a national hot-spot of greenhouse gas emissions.

In this study we evaluated potential trade-offs between water table management practices for minimising peat wastage and greenhouse gas emissions, whilst seeking to sustain romaine lettuce production, one of the most economically relevant crops in The Fens.   To identify the impact of temperature and water table management on crop yield and greenhouse gas emission, we measured romaine lettuce yield, the rate of peat wastage through CO_2, CH_4 fluxes, and DOC release on agricultural fen peat at two temperatures (ambient and + 2°C) and three water table levels (-30 cm, -40 cm and -50 cm below the surface) in a controlled environment experiment .

We show that increasing the water table from the field level of -50 cm to -40 cm and -30 cm reduced CO_2 emissions, did not affect CH_4 fluxes, but increased production of DOC. Warming of 2°C increased both romaine lettuce yield and peat decomposition through the loss of carbon as CO_2 and DOC. Unfortunately, raising the water table from -50 cm was found to significantly reduce romaine lettuce yield, indicating that the optimal conditions for this crop will continue to degrade fen peatlands. Raising the water table would preserve the agricultural peat for longer, however, at the expense of crop yield.

4.1 Introduction

Global emissions of GHG from croplands are estimated to be 1994 +/- 2172 Tg CO_2 equivalent, with 32% coming from peatland cultivation (Carlson et al., 2016), despite peatlands being a small part of the total cultivated area. The disproportionate contribution of peatland cultivation to GHG emissions is linked to their very large carbon stores, which accounts for 30% of the total soil carbon being found in peatlands globally (Global Environmental Centre, 2008). In the UK, 40% of peatlands have been drained for agricultural use (Dixon et al., 2014), and some of the fastest rates of peat wastage and GHG emissions are found on drained and cultivated lowland peatlands, such as in East Anglian Fenlands (The Fens, Fig. 4.1). This is a lowland area of peat covering around 3890 km^2 of Cambridgeshire, Lincolnshire, West Norfolk and West Suffolk, and includes some of the last deep (>40 cm) peats remaining in the UK that are used in agriculture (NFU, 2019). This area is commercially very important for horticulture, supplying 37% of total vegetable production in England (NFU, 2019), with high value fast-growing horticultural crops with large water requirements such as romaine lettuce, radishes and celery being grown, along with root crops such as sugar beet and potatoes together with other vegetables (Darby, 1956; Dawson et al., 2010). Drainage, fertilization, and intensive cultivation for crop production results in high rates of peat wastage by microbial aerobic decomposition (Global Environmental Centre, 2008), turning The Fens into a national hotspot of GHG emissions (Fig. 4.1). The deep peats, which are the focus of the present study, are estimated to release between 17-50 tonnes CO_2 equivalent ha^{-1} each year at landscape-scales (Fig. 4.1). This GHG flux is dominated by CO_2, as CH_4 fluxes from these peats under current water-table management are negligible, although fluxes of the potent greenhouse gas N_2O (nitrous oxide) can sometimes be important (Taft et al., 2018).

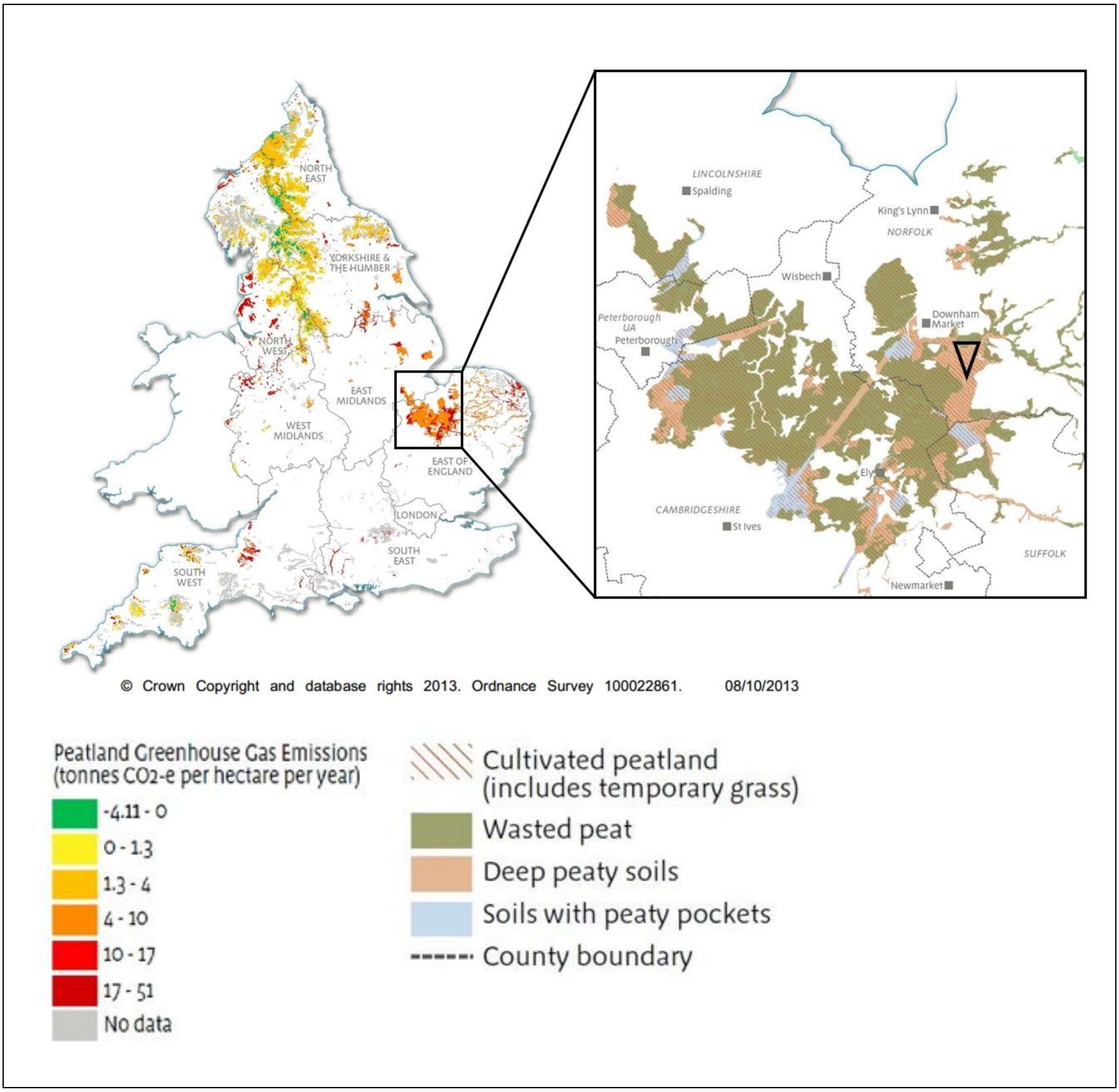


Figure 4.1: Sampling site location in East Anglian Fenlands. The legend shows estimated GHG emissions from peatlands in England and peat quality of the Fens. The approximate location of the sampling field is indicated by a black triangle.

Source: Natural England, 2010

It has been predicted that two thirds of the peat in The Fens will be lost by 2050 due to oxidative degradation (Burton and Hodgson, 1987), threatening the future production of food crops in this region. It is therefore timely to evaluate alternative management practices that seek to sustain crop yields whilst slowing the rate of peat degradation. Recent estimates of rates of peat loss from the East Anglian fens range from 0.33–0.75 cm depth per year (Taft et al., 2017), with rates generally increasing in agricultural land from 0.44 cm per year in shallow peat to 0.62 cm per year in deep peat (Evans et al., 2016).

The position of the water table is a main control on GHG emissions, especially for CO_2 and CH_4 (Taft et al., 2017; Kandel et al., 2018; Liimatainen et al., 2018; Taft et al., 2018; Peacock et al., 2019). In undisturbed peatlands higher water tables are frequently associated with reduced CO_2 loss, but can cause substantial increases in CH_4 emissions (Nykanen et al., 1995, Strack et al., 2004, Jungkunst et al., 2008, Dinsmore et al., 2009, Yrjälä et al., 2011, Hou et al., 2013, Peacock et al., 2019). However, raising the water table in The Fens is expected not only to extend the lifespan of these agricultural peats, but also considerably lower their CO_2 emissions (Karki et al., 2016; Taft et al., 2018; Peacock et al., 2019).

The use of a higher water table level, however, might negatively affect crop yield (Xu et al., 2013), limiting its adoption by farmers. In a fen grassland, maximal yield was achieved with the water table at a depth of between -40 cm to -50 cm, while raising it to -30 cm reduced peat decomposition by 30-40%, with only a 10% fall in grass productivity (Renger et al., 2002). However, these effects are not generalizable, as impacts of water table manipulation on horticultural crop yields have given mixed results, depending on the crop studied. Soybean yields were 5% lower with the water table at -30 cm compared to -50 cm to -60 cm (Matsuo et al., 2017), and Ferreira et al. (2017) found that water table position (two depths: -36 cm and -76 cm) affected potato root distribution, but did not impact tuber mass. Previous studies by our research team, on high value horticultural crops, with a high water content and high water requirements, showed that raising the water table of fenland peat from -50 cm to -30 cm increased the total fresh biomass of radish by 33% (Musarika et al., 2017), but lowered fresh biomass of celery by 19% (Matysek et al., 2019). These crop specific responses require the impact of different water table levels on yield to be investigated across the most economically relevant crops.

In the present study we set out to investigate whether changes to the current fenland water table position can lower peat heterotrophic respiration and DOC production, and potentially increase carbon assimilation by another high-value high water-demand crop, romaine lettuce. This knowledge is very important in providing science evidence for policymakers to guide land management strategies that reduce greenhouse gas emissions, and guidance for farmers to decide on management practices that can maintain yield while reducing the peat wastage.

Aside from drainage, since peat oxidation is a microbial-driven biological process, peat wastage is normally increased at higher temperatures (Ziegler et al., 2013). Due to climate change the average temperature in the UK is expected to rise by 0.3-4.8°C by the end of this century (relative to 1986-2005) (IPCC, 2014a). In the East of England this increase is expected to be between 1.3°C to 7.5°C in summer (Jenkins et al., 2003). Rising temperatures can enhance soil organic matter decomposition and emissions of GHG, but also accelerate plant growth and CO_2 absorption by plants (Rustad et al., 2001; Adaptation Sub-Committee, 2016; Ostberg et al., 2018). The net response of soil C stocks and fluxes to rising temperatures may not be uniform between different land uses and different temperatures, and may depend on the composition and decomposition state of peat (Duval and Radu, 2018). The rate of peat decomposition was the same for cropland, grassland and forested land when incubated at 10°C, but at 20°C the croplands showed higher rates of decomposition than forested peat (Bader et al., 2018). Given the climate-change driven warming of The Fens, the combined effect of warmer temperature and water table levels should be investigated. In the UK, global warming is expected to cause a sea level rise of 0.1– 1.2 m by the end of this century (as compared to 2000 values) (Palmer et al., 2018). Therefore, it is important to minimise further subsidence of the Fens, which are already at or below current sea level (Darby, 1956).

In addition to loss by gaseous emissions of CO_2 and CH_4, C may be lost from agricultural peats into water bodies as DOC. In the UK, DOC is a substantial component of total terrestrial C flux, especially in areas with extensive organic soils (Baker et al., 2008; Gibson et al., 2009; Worrall et al., 2009; Worrall et al., 2012). The need for drainage of the Fens means that organic-rich waters from the peats are pumped out into the river system, contributing to DOC loss. The concentration of DOC in the soil solution is dependent on the balance between production from soil organic matter and consumption by soil microorganisms (Liu et al., 2016). DOC in water bodies may eventually be converted to CO_2 (contributing to 'offsite emissions') via photodegradation and biodegradation (Peacock et al., 2019). DOC concentrations in UK river and lake catchments are on the rise (Freeman et al., 2001; Worrall, et al., 2003; Worrall et al., 2004a; Worrall et al, 2004b), and this increase is not always easy to explain (Worrall and Burt, 2007; Evans et al., 2012). Loss of DOC in drainage water is often ignored by studies documenting C dynamics in peatlands despite its potential importance in determining whether an ecosystem is a C sink or a source. Peatlands export a significant amount of DOC, with 20% of all terrestrial DOC exported to sea coming from peat soils (Fenner et al., 2007). The water table position may play a key role in DOC production in agricultural peats, which has implications for the C balance of the Fens, where the water level is actively adjusted. Research shows that agriculturally-used peat of the Fens experienced seasonal DOC content fluctuations which were related to the water table level – this dynamic was not present in the neighbouring rewetted peatland site (Peacock et al., 2019). However, there are also studies reporting no link between water table depth and DOC content in peat and groundwater (Chow et al., 2006; Frank et al., 2017; Lundin et al., 2017; Tiemeyer and Kahle, 2017). Studies often use ditch water samples to estimate DOC production in peat - this could lead to inaccurate flux estimates as ditch concentrations were shown to be lower than groundwater DOC concentrations (Tiemeyer and Kahle, 2017). To fill knowledge gaps in DOC dynamics on agricultural peatlands, in the present study we measured DOC content in both pore water and drainage water.

Following our previous work (Musarika et al., 2017; Matysek et al., 2019) on drained agricultural fen peat, we tested the impact of the effects of the same water table levels (-30 cm and -50 cm) but also of an intermediate water table (-40 cm) on shoot and root production of another relevant crop (romaine lettuce). We also studied peat C loss as CO_2, following our previous studies, determining NEE, ER, and Rh, together with CH_4 fluxes, as well as a more in-depth study of DOC production and fluxes. Soil respiration is the CO_2 flux from bare (unplanted) soil, whereas NEE is the rate of CO_2 absorption by the plant and ER the rate of CO_2 respiratory loss in the dark. Romaine lettuce was chosen for this experiment, since it is among the most profitable and most frequently grown crops by the farmer (Martin Hammond, pers. comm.), its value having increased in recent years (Defra, 2014; Defra, 2016). In the UK, lettuce production has been shifting towards varieties with a large profit margin which do not require large cropping area, such as certain small varieties of romaine lettuce (Schoen and Lang, 2016). This crop has a high water requirement and is densely planted in field (which suits the design of the experiment in peat cores). We hypothesized that raising the water table would decrease Rh, NEE and increase GPP and CH_4 emissions and that an intermediate water table of -40 cm would provide a good compromise between limiting peat wastage and achieving a good crop yield. On the basis of our previous results obtained in the experiment on celery, we also hypothesized that warming of 2°C would raise emissions of the two GHG gases (i.e. CO_2 and CH_4) and the DOC concentration in the soil water but would also enhance the growth of romaine lettuce.

4.2 Methods

4.2.1 Field site

The peat cores used in this experiment were collected from a field on Rosedene Farm in Methwold Hythe, Norfolk in March 2017 (Fig. 4.1). The site is situated on deep (>40 cm) peat within the East Anglian Fenlands, in the southeast of the UK, and has a yearly rainfall below 600 mm (Evans et al., 2016) and a mean annual temperature of 10°C (Cumming, 2018). A substantial portion of the Fens lies at or below the sea level, its lowest point being at Holme Fen: -2.7 m (Wildlife Trust Countryside Centre, Cambridge). In the field, a water table position at -50 cm is maintained through a network of river-linked drainage channels and water-pumping stations. The sampling site is described in more detail in Matysek et al. (2019).

4.2.2 Soil core sampling and experimental design

A total of 64 soil cores of diameter 11 cm were collected to a depth 60 cm below the surface. The collection was performed using PVC pipes, which were inserted into the soil, as described in Matysek et al. (2019), and excavated to preserve the existing soil structure. Pipe plugs were then inserted at the base of each core to retain the field soil moisture (Fig. 4.2).

Figure 4.2: Peat cores with romaine lettuce grown with different water table depths a) after 5 weeks; b) after 8 weeks; c) after 12 weeks; d) washed lettuce roots following harvest.

After collection, the 64 cores were placed in two CONVIRON BDW 40 growth chambers (Controlled Environments Ltd., Winnipeg, Manitoba, Canada) at the Sir David Read Controlled Environment Facility, University of Sheffield, UK. Romaine lettuce was planted in half of the cores and grown for 12 weeks while the other cores were left unplanted (Fig. 4.3). During these 12 weeks NEE, GPP, and ER were measured weekly in the planted cores, and Rh was measured in the unplanted cores. The light settings were the same for both growth chambers, however, the actual PAR received by plants in both chambers varied between 670-740 µmol m^{-2} s^{-1} due to technical issues with the chamber functioning. Relative humidity inside the chambers was maintained at 70%, which is similar to the relative humidity observed at the field site (i.e. 70-80% from March to May; Cumming, 2018). The CO_2 level in both chambers was maintained at the ambient concentration of around 440 ppm.

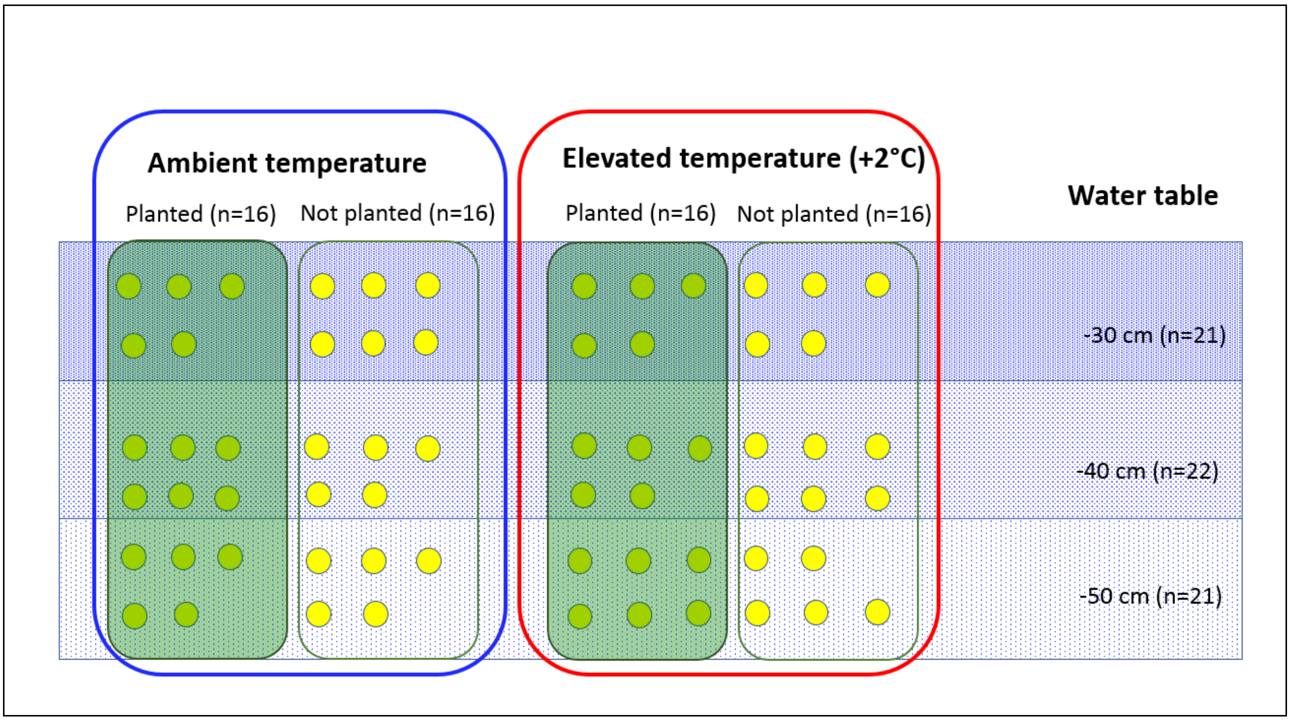


Figure 4.3: Multifactorial design of the experiment including two temperature treatments (ambient and elevated), two planting treatments (planted, not planted) and three water table treatments (-30 cm, -40 cm and -50 cm below the surface). Each dot represents one peat core. Total number of cores is 64.

The chambers regulated air temperature in real time with an accuracy of ±0.5°C. Inside these chambers, the cores (planted and unplanted) were subjected to a multifactorial manipulation (Fig. 4.3) of:

- Water table at three levels: -30 cm, -40 cm and -50 cm below the surface
- Temperature: ambient and elevated (+2°C)
- Cropping: planted and fallow

The water table in each core was monitored with the use of 20 mm diameter drainage pipes with holes every 1 cm protected by fine nylon mesh to prevent clogging of the holes with soil. The water table depth was measured once a day with a marked stick and distilled water was added through the drainage pipe if necessary to maintain the required water level (usually every 1-2 days). There were no instances for the duration of the experiment of water needing draining from peat columns. Soil water content was measured in the top 12 cm every week with a Campbell Scientific soil moisture probe (model CS655, Campbell Scientific, Logan, Utah, USA).

The ambient temperature used was selected as the average daytime temperature collected from a meteorological station in the field over the duration of three years (Cumming, 2018), during the time of the year that lettuce crops are established (romaine lettuce is planted during February and March) (Fig. 4.4). Both daytime and night time temperature settings were based on these field data, and 12 h day length was used throughout. The daytime temperature was set at 8°C in weeks 1-4 (4°C at night), 11°C in weeks 5-6 (6°C at night), 13°C in weeks 7-8 (7°C at night) and 14°C thereafter (8°C at night in weeks 9-10, and 9°C in weeks 11-12). The elevated temperature treatment followed the same regime, but with both day and night temperatures +2°C higher. This was chosen to approximate the average of the RCP 4.5 scenario that predicts a temperature rise of 1.7°C to 3.2°C before the end of this century relative to years 1850-1900 (IPCC, 2014a; Palmer et al., 2018). We are already seeing spring-time temperature increases above the long-term averages, of this magnitude or larger some years in The Fens. For example, weather station data for Wisbech in 2019 recorded mean daytime temperature in February of 11.8°C compared to a long-term average of 6.8 °C, and for March 2019, 12°C compared to the long-term average of 10°C (Accuweather.com, 2019).

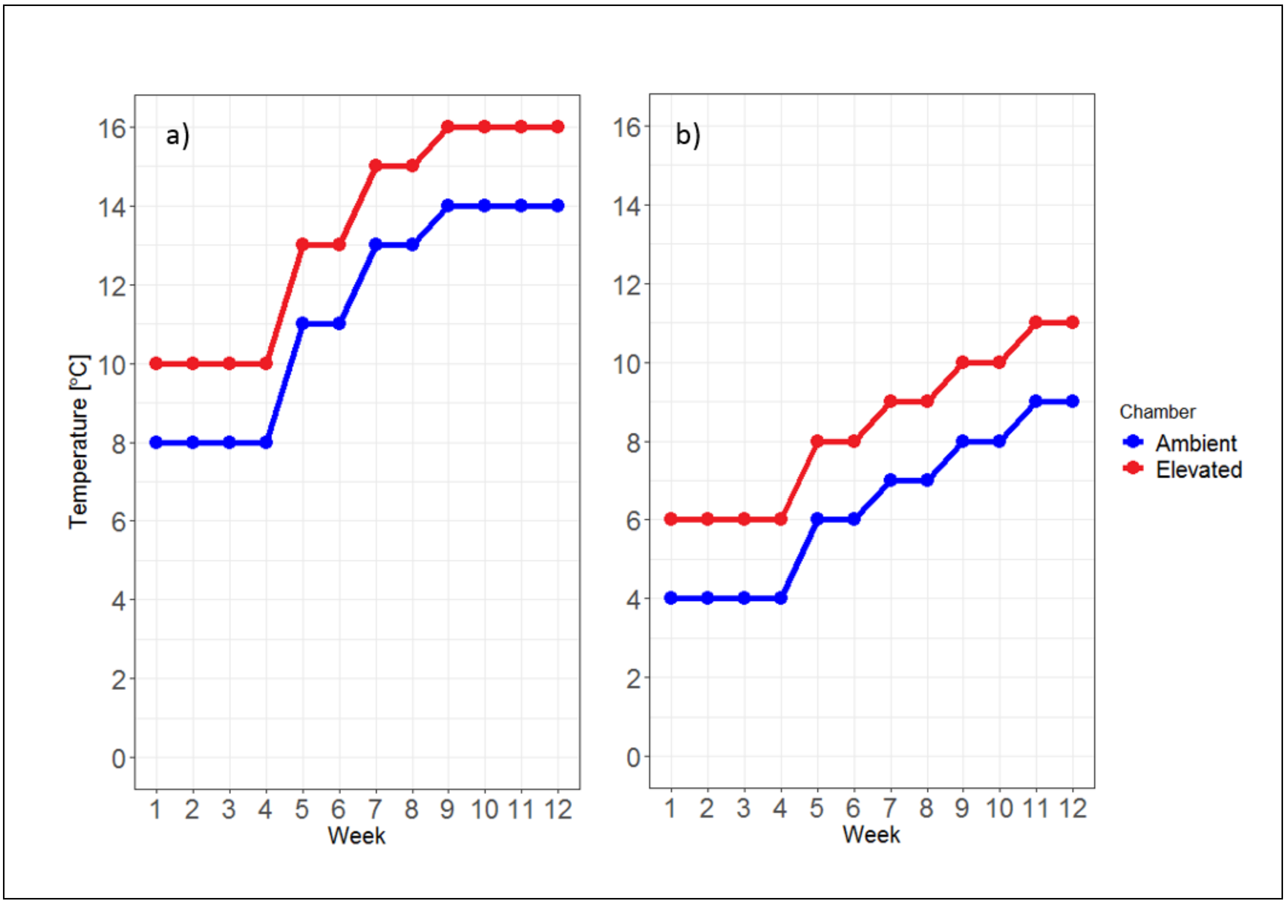


Figure 4.4: Day (a) and night (b) temperature settings for ambient and elevated (ambient + 2 °C), with 12 h days.

Romaine lettuce seedlings were germinated for around 3 weeks in growth chambers on peat collected from the sampling site, and at the start of the first week of the experiment one pre-germinated seedling was planted into each peat core. We placed the cores in random order every week in order to prevent specific chamber effects (related to the position of each core in each chamber).

To simulate field conditions as closely as possible, we applied the same fertiliser and dose that the farmer uses for romaine lettuce. All cores were fertilised with liquid Chafer 15-5-10 (N:P:K mass ratio of 15:5:10, the numbers refer to weight of each component on a w/v basis [g/100 ml]) at the rate of 1000 l ha^{-1} (0.95 ml per core) and Chafer Starter Solution Plus 11-38-3 (NPK + trace elements of Cu, Mn, Zn) at the rate of 0.19 ml per core. The cores were fertilised a day before planting the seedlings and the starter solution was added when the seedling were transferred into the cores.

4.2.3 Greenhouse gas fluxes

CO_2 and CH4 concentrations in the headspace of the cores were collected once a week for 11 weeks using an LGR Ultra Portable Gas Analyser GGA-30p (Los Gatos Research, Mountain View, CA, USA). Two custom-made PVC chambers both with a volume of 2.8 l were used to record change in gas concentration over time and calculate the fluxes, one transparent for light measurements to measure Rh in the unplanted cores and NEE in the planted cores (and estimate GPP) and an opaque chamber for dark measurements to measure the ER in the planted cores. Gross Primary Productivity was estimated as GPP=ER-NEE. The rates of change in CO_2 and CH_4 concentrations in the chambers over time were used to estimate GHG fluxes as described in McEwing et al. (2015).

4.2.4 Concentrations of DOC, NH_4^+ and NO_3^- in topsoil pore water

Water samples were collected in weeks 4, 6, 8 and 11 from two sources: the drainage pipe used for the water table measurements (using a syringe) and directly from soil pores using Rhizon soil moisture samplers (Rhizosphere Research Products, Wageningen, Netherlands), inserted in the top 10 cm of soil. Samples for the DOC analysis were filtered on Whatman 0.7 µm GD/X glass fibre syringe filters and analysed on a Sievers 5310C Carbon Analyser. The detection limit of this Carbon Analyzer is 4 ppb and the calibration standards were 1000 mg C l^{-1} or 500 mg C l^{-1} potassium hydrogen phthalate.

Samples for the NH_4^+ and NO_3^- analysis were filtered on 0.45 µm syringe filters and frozen right after sampling until analysis. Concentrations of NH_4^+ and NO_3^- were determined using the colorimetric methods described by Mulvaney (1996) and Mackereth et al. (1989), respectively. The absorbance was measured at 667 nm for NH_4^+ and at 543 for NO_3^- on 7315 UV/Vis spectrophotometer.

4.2.5 Romaine lettuce harvest and root extraction

After growing for 12 weeks in the peat cores the romaine lettuce plants were harvested and fresh biomass measured, dried at 80°C for 24 hours and dry biomass weighed. The soil columns were then frozen in order to prevent root decomposition and to facilitate extraction of the peat. On partial defrosting, the peat cores were cut into 10 cm depth increments and roots were separated by washing under running tap water using a 425 µm sieve, then oven-dried at 80°C for 24 hours and weighed.

4.2.6 Statistical analysis

Statistical analysis was performed using the open source program R, version 3.3.1 (R Core Team 2016). A two-way ANOVA was employed to determine the effects of water table and temperature treatments on romaine lettuce biomass. We used two types of models to analyse the GHG data: linear models and linear mixed models. The linear mixed models were applied using the lme4 package (Bates, Maechler and Bolker, 2014), including ‘week’ and ‘core’ as random effects to avoid temporal and spatial pseudoreplication (i.e. sampling the same cores multiple times during the experiment). These linear mixed models were used for testing the effects of water table level, soil water content, crop presence and temperature on DOC concentrations in water and emissions of CO_2 and CH_4, with ‘week’ and ‘core’ as random effects. Outliers, as determined by the Cook’s distance, were removed from the CH_4 data. In the analyses in which the lme4 package was used, $\chi 2$ is reported in the place of the F-value. We also averaged

CO_2 and CH_4 fluxes for the entire experiment and applied a simple linear model: doing so removed pseudoreplication. The linear mixed models and the linear models were then compared to test if the averaged models could be used in place of linear mixed models. The adequacy of all models was assessed by visual inspection of residual plots. The CH_4 flux data used in the linear modelling was log-transformed, since its distribution did not meet the assumptions of linear models. When mixed effects models were used, the statistical significance of each factor was determined by likelihood ratio tests performed with the ANOVA function between the full model and the model without the fixed factor. When water table level was significant across different treatment's groups, the difference among Rh, ER, NEE, GPP, CH_4 and DOC with three water table treatments was estimated using a post hoc Tukey test.

4.3 Results

Romaine lettuce fresh and dry weights were significantly higher (by 38% and 42%, respectively) under elevated temperature than under ambient temperature (Table 4.1, Fig. 4.5). Both biomass measures were significantly affected by the water table: the highest yields were in the -50 cm treatment being 21% greater than in the -40 cm treatment and 32% higher than in the -30 cm treatment (Fig. 4.5).

	df	F-value	P-value
Shoot fresh weight			
Water table	2,24	12.33	**<0.001 *****
Temperature	1,24	28.66	**<0.001 *****
Water table*Temperature	2,24	0.81	0.456
Shoot dry weight			
Water table	2,24	5.01	**0.015 ***
Temperature	1,24	58.19	**<0.001 *****
Water table*Temperature	2,24	2.3	0.121
Tap root dry weight			
Water table	2,24	8.62	**0.002 ****
Temperature	1,24	43.28	**<0.001 *****
Water table*Temperature	2,24	0.85	0.44
Total root dry weight			
Water table	2,21	6.36	**0.007 ****
Temperature	1,21	33.98	**<0.001 *****
Water table*Temperature	2,21	0.77	0.477
Root dry weight in top 10 cm			
Water table	2,22	6.84	**0.005 ****
Temperature	1,22	31.54	**<0.001 *****
Water table*Temperature	2,22	0.8	0.46
Root dry weight 10 cm – 30 cm			
Water table	2,22	15.13	**<0.001 *****
Temperature	1,22	58.4	**<0.001 *****
Water table*Temperature	2,22	5.19	**0.014 ***
Root dry weight below 30 cm			
Water table	2,22	4.89	**0.018 ***
Temperature	1,22	0.55	0.467
Water table*Temperature	2,22	0.83	0.452
Root dry weight in bottom 40 cm			
Water table	2,23	5.43	**0.012 ***
Temperature	1,23	1.64	0.212
Water table*Temperature	2,23	1.43	0.26
Root:shoot ratio			
Water table	2,21	1.09	0.354
Temperature	1,21	0	0.998
Water table*Temperature	2,21	2.02	0.158

Table 4.1: ANOVA test results for effects of environmental variables (three water table positions, ambient and elevated temperature, and their interactions) on different components of lettuce biomass at harvest using linear models. Tap root is the thickest root, with lateral roots removed. The root:shoot ratio was calculated on dry biomass. * - may be significant; ** - significant; *** - highly significant; df – degrees of freedom.

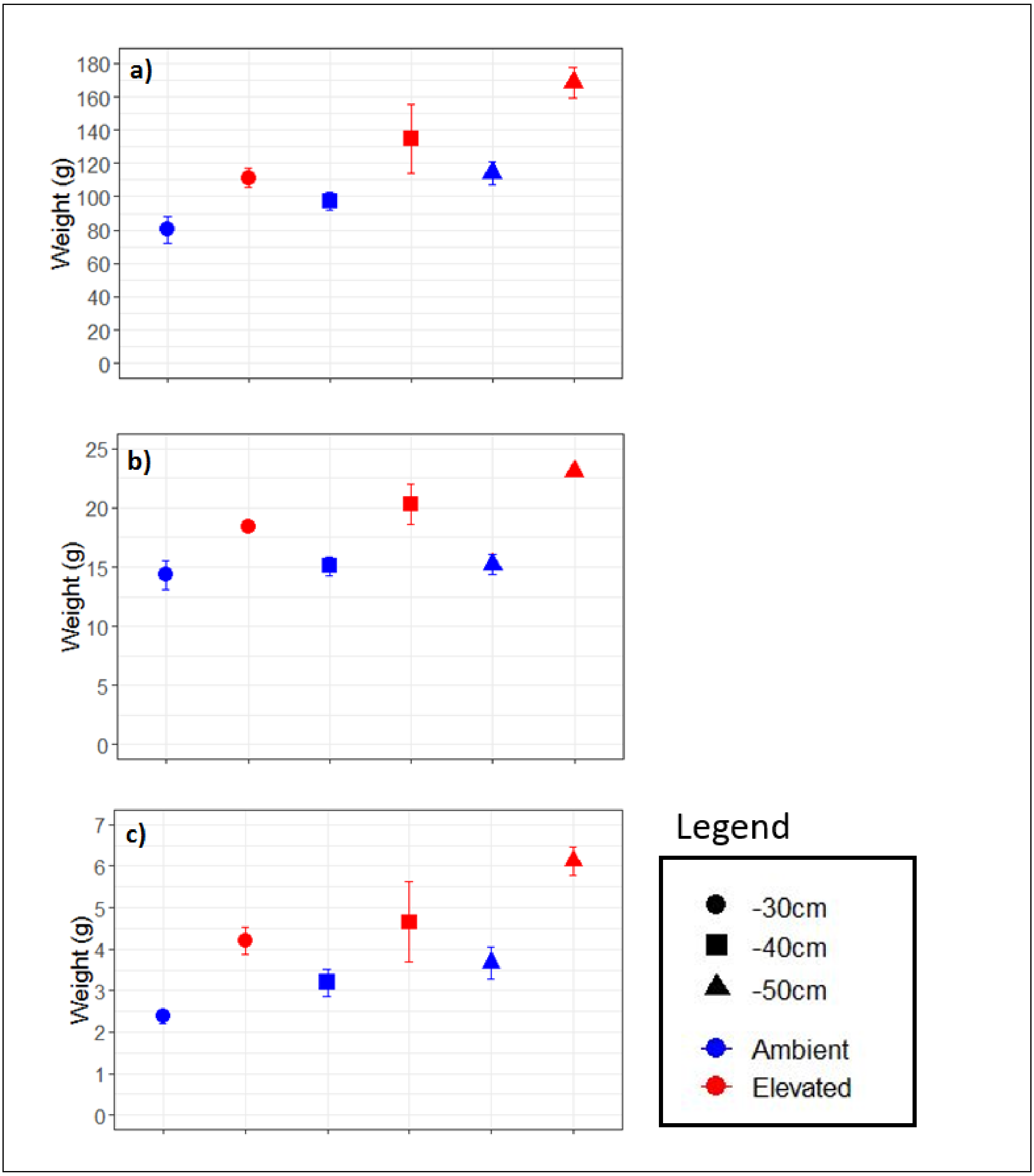


Figure 4.5: Romaine lettuce biomass (mean ± 1 standard error) responses to temperature and water-table manipulations. There are two temperature settings: ambient and elevated (ambient + 2°C). Water table levels are -30 cm, -40 cm and -50 cm. In all cases, n=5 apart from: '-40 cm Ambient' and '-50 cm Elevated' where n=6. a) Shoot fresh weight, b) Shoot dry weight, c) Root dry weight.

Root biomass responses were similar to those of the shoots, with root dry root weight being 40% higher in the elevated temperature treatment than in the ambient one (Fig. 4.5) and was reduced by raising the water table level (e.g. 27% lower in the -30 cm water table treatment than the -50 cm treatment, Fig. 4.5). There were no statistically significant differences in total root biomass between -30 cm and -40 cm and between -40 cm and -50 cm water table levels (Table 4.2). Dry root biomass in the top 10 cm of soil layer was significantly higher (by 60%) in the elevated temperature treatment (Table 4.1) and differed only between the -30 cm and -50 cm water tables (Table 4.2), being lower at -30 cm. Root biomass below -30 cm was not affected by temperature (Table 4.1). The root:shoot ratio was not affected by any of the treatments (Table 4.2). There were no significant interactions between temperature and water table in explaining variations in biomass.

	t-value	**P-value**
Shoot fresh weight		
WT (-30 cm) & WT (-40 cm)	2.166	0.0979
WT (-30 cm) & WT (-50 cm)	4.906	**<0.001 *****
WT (-40 cm) & WT (-50 cm)	2.690	**0.0329 ***
Shoot dry weight		
WT (-30 cm) & WT (-40 cm)	1.467	0.3242
WT (-30 cm) & WT (-50 cm)	3.082	**0.0136 ***
WT (-40 cm) & WT (-50 cm)	1.583	0.2720
Tap root dry weight		
WT (-30 cm) & WT (-40 cm)	1.485	0.3155
WT (-30 cm) & WT (-50 cm)	4.004	**0.00149 ****
WT (-40 cm) & WT (-50 cm)	2.478	0.0519
Total root dry weight		
WT (-30 cm) & WT (-40 cm)	1.705	0.2266
WT (-30 cm) & WT (-50 cm)	3.961	**0.002 ****
WT (-40 cm) & WT (-50 cm)	2.387	0.0652
Root dry weight in top 10 cm		
WT (-30 cm) & WT (-40 cm)	1.604	0.2648
WT (-30 cm) & WT (-50 cm)	3.658	**0.0038 ****
WT (-40 cm) & WT (-50 cm)	2.111	0.1107
Root dry weight below 30 cm		
WT (-30 cm) & WT (-40 cm)	-0.216	0.9747
WT (-30 cm) & WT (-50 cm)	2.687	**0.0345 ***
WT (-40 cm) & WT (-50 cm)	2.866	**0.0233 ***
Root dry weight 10 cm -30 cm		
WT (-30 cm) & WT (-40 cm)	3	**0.017 ***
WT (-30 cm) & WT (-50 cm)	5.9	**<0.001 *****
WT (-40 cm) & WT (-50 cm)	3.264	**0.01 ****

Table 4.2: Post-hoc Tukey test results for the significance of effects of water table levels on romaine lettuce shoot and root biomass at harvest. Displayed are t-values and p-values of the tests. Tap root dry weight is for the thickest root, with lateral roots removed.

Soil water content was significantly lower in the elevated than ambient temperature treatment (by 8%), in planted compared to unplanted cores (by 11%) and was affected by the water table position (Table 4.3, Fig. 4.6). As expected, soil water content was significantly lower in the -50 cm treatment when compared to -30 cm (by 19%) and -40 cm (by 14%) (Table 4.4).

	lmer			lm		
CH_4 fluxes	**df**	**χ2**	**P-value**	**df**	**F-value**	**P-value**
Planting	1	2.76	0.1	1, 49	4.34	**0.042 ***
Temperature	1	9.64	**0.002****	1, 49	4.53	**0.038 ***
Water table	2	4.33	0.115	2, 49	22.17	**<0.001 *****
Soil water content	1	3.34	0.06741	1, 59	4.61	**0.036 ***
Water table*Temperature	2	2.32	0.313	2, 49	1.31	0.278
Temperature*Planting	1	1.71	0.191	1, 49	2.07	0.156
Water table*Planting	2	0.93	0.628	2, 49	1.9	0.16
Soil respiration (Rh)						
Temperature	1	5.23	**0.022 ***	1, 25	4.87	**0.037 ***
Water table	2	18.2	**<0.001 *****	2, 25	21.94	**<0.001 *****
Water table*Temperature	2	0.02	0.989	2, 25	0.05	0.95
Soil water content	1	1.52	0.2181	1, 29	28.64	**<0.001 *****
Net Ecosystem Exchange (NEE)						
Temperature	1	5.37	**0.02 ***	1, 26	9.23	**0.005 ****
Water table	2	5.08	0.079	2, 26	1.92	0.167
Soil water content	1	0.19	0.665	1, 30	0.06	0.812
Water table*Temperature	2	0.18	0.913	2, 26	0.1	0.909
Gross Primary Production (GPP)						
Temperature	1	24.58	**<0.001 *****	1, 26	31.97	**<0.001 *****
Water table	2	0.39	0.822	2, 26	0.35	0.709
Soil water content	1	0.23	0.6343	1, 30	2.64	0.115
Water table*Temperature	2	0.44	0.805	2, 26	0.48	0.63
Ecosystem respiration (ER)						
Temperature	1	13.4	**<0.001 *****	1, 26	35.35	**<0.001 *****
Water table	2	1.94	0.379	2, 26	4.26	**0.025 ***
Soil water content	1	0.53	0.4674	1, 30	8.49	**0.007 ****
Water table*Temperature	2	2.51	0.286	2, 26	2	0.155
Soil water content						
Temperature	1	18.86	**<0.001 *****	1, 59	12.33	**<0.001 *****
Water table	2	25.13	**<0.001 *****	2, 59	30.61	**<0.001 *****
Planting	1	8.39	**<0.001 *****	1, 59	26.87	**<0.001 *****

Table 4.3: Effects of environmental variables and their interactions on gas fluxes using both the linear mixed model (lmer) (which included ‘week’ and ‘core’ as random effects, to take into account the temporal and spatial pseudoreplication) and linear models (lm) (which were applied to the fluxes averaged over the entire experiment). The experiment lasted 12 weeks and the GHG were measured eight times (every week or every two weeks). The total number of measurements used in the lmer model was n=512 (for CH_4, Rh and soil water content) and n=256 (for GPP, ER and NEE). Rh – soil respiration; NEE – Net Ecosystem Exchange; GPP – Gross Primary Production; ER – ecosystem respiration.

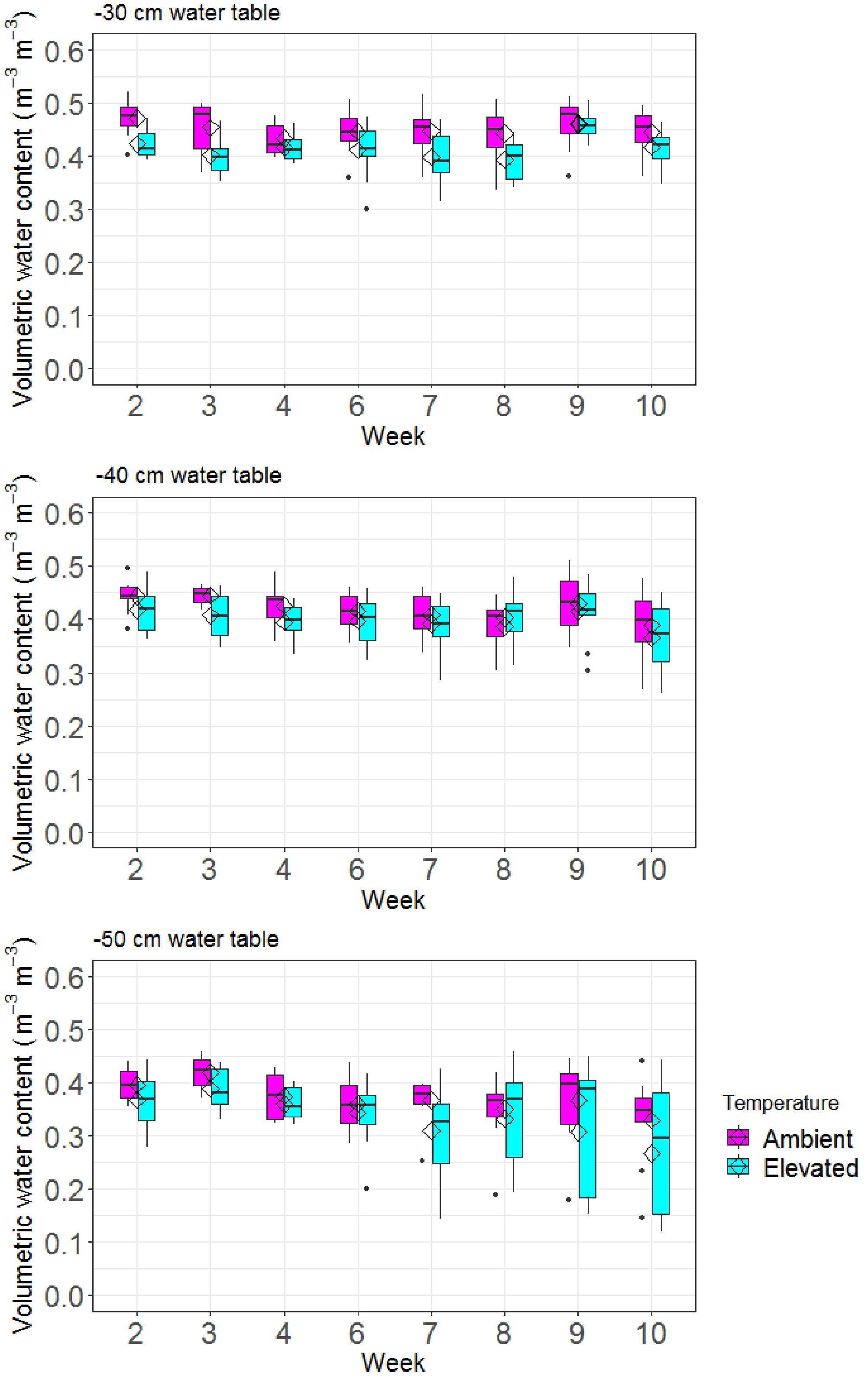
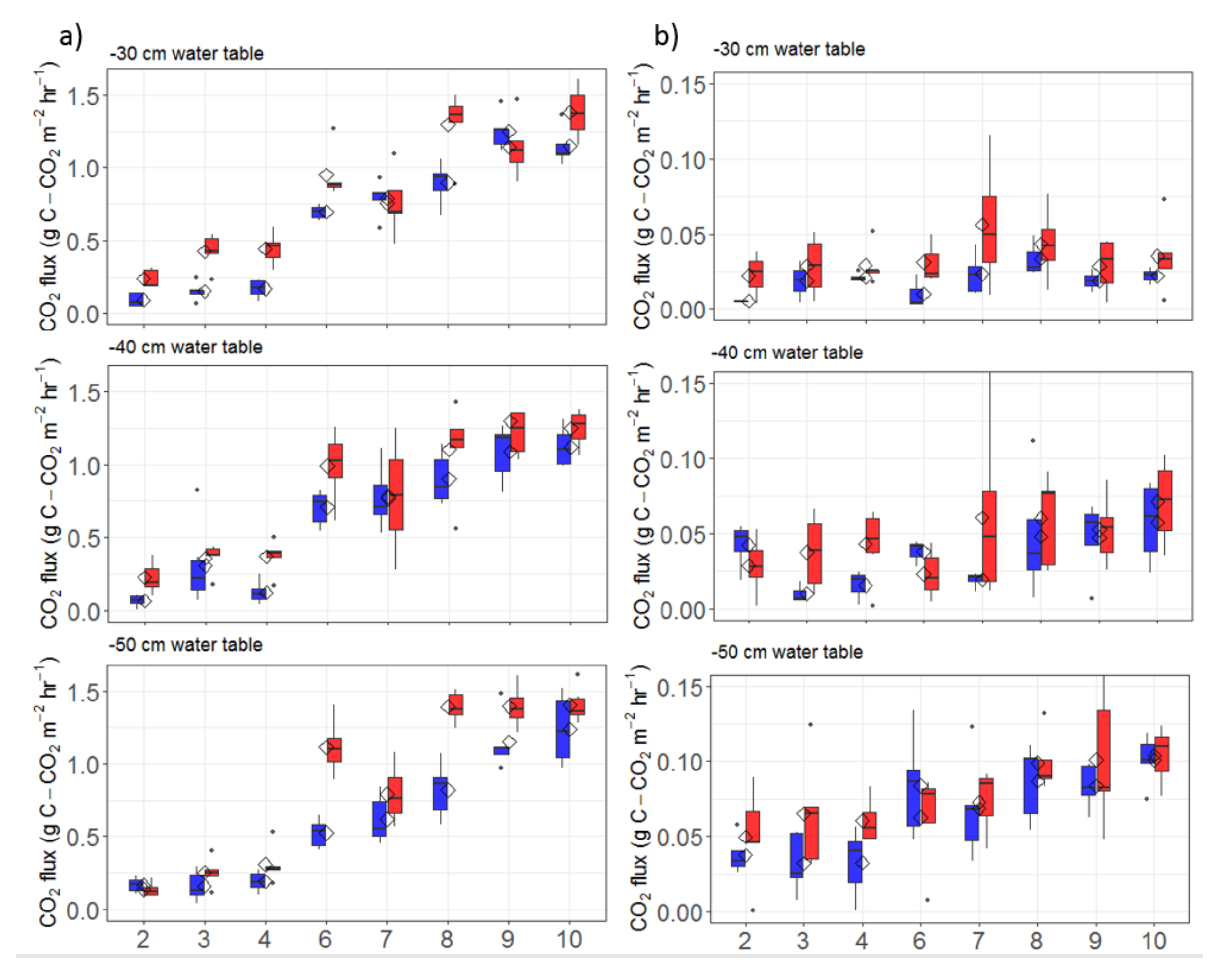


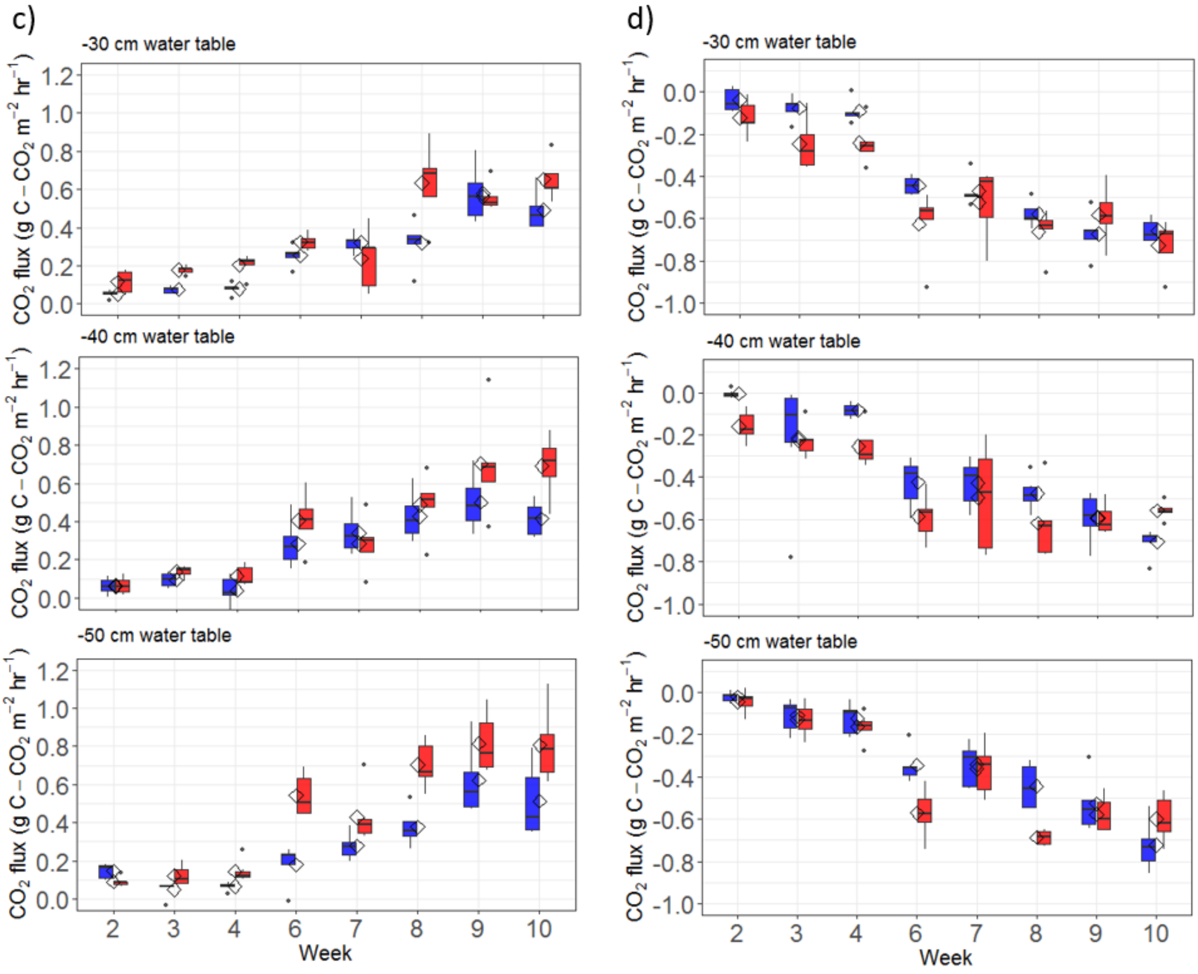
Figure 4.6: Soil water content weakly averages in three water table levels (-30 cm, -40 cm and -50 cm) and two temperatures. Colours indicate: ambient (purple) and elevated (ambient +2°C) (blue).

	t-value	**P-value**
CH_4		
WT (-30 cm) & WT (-40 cm)	-1.426	0.3356
WT (-30 cm) & WT (-50 cm)	-3.976	**<0.001 *****
WT (-40 cm) & WT (-50 cm)	-2.547	**0.0368 ***
Soil respiration (Rh)		
WT (-30 cm) & WT (-40 cm)	1.859	0.172
WT (-30 cm) & WT (-50 cm)	6.437	**<0.001 *****
WT (-40 cm) & WT (-50 cm)	4.716	**<0.001 *****
Gross Primary Production (GPP)		
WT (-30 cm) & WT (-40 cm)	0.528	0.8582
WT (-30 cm) & WT (-50 cm)	3.166	**0.0106 ***
WT (-40 cm) & WT (-50 cm)	2.697	**0.0313 ***
Ecosystem respiration (ER)		
WT (-30 cm) & WT (-40 cm)	-0.071	0.997
WT (-30 cm) & WT (-50 cm)	2.030	0.125
WT (-40 cm) & WT (-50 cm)	2.148	0.1
Soil water content		
WT (-30 cm) & WT (-40 cm)	-2.121	0.0942
WT (-30 cm) & WT (-50 cm)	-7.266	**<0.001 *****
WT (-40 cm) & WT (-50 cm)	-5.237	**<0.001 *****

Table 4.4: Post-hoc Tukey test results for effects of water table levels on GHG emissions and the water content of soil. Displayed are t-values and p-values of the test.

Soil respiration was increased (by 18%) under elevated temperature, and was affected by water table, both of these variables having significant effects in both the linear mixed models and the linear models, (Table 4.3; Fig. 4.7). The Rh flux was 40% higher in the -50 cm than the -40 cm water table level and 60% higher in the -50 cm than the -30 cm water level (Table 4.4, Fig. 4.7). Ecosystem respiration was significantly 46% higher in the elevated temperature treatment than in the ambient temperature and it was affected by water table in the linear model, but not in the linear mixed model (Table 4.3, Fig. 4.7). The post-hoc test showed no significant differences between the Rh at water table level -30 cm and -40 cm, but significance differences to the -50 cm treatment (Table 4.4, Fig. 4.7). Net ecosystem exchange was 20% lower in the elevated temperature treatment than in the ambient and was unaffected by the water table level in both the linear and the mixed linear model (Table 4.3, Fig. 4.7). Gross Primary Production was higher by a third in the elevated temperature treatment (compared to the ambient conditions) and unaffected by the water table position (Table 4.3, Fig. 4.7).




c)
-30 cm water table
-40 cm water table
-50 cm water table
CO_2 flux (g C – CO_2 m^{-2} hr^{-1})
0.0
0.2
0.4
0.6
0.8
1.0
1.2
2
3
4
6
7
8
9
10
Week
d)
-30 cm water table
-40 cm water table
-50 cm water table
CO_2 flux (g C – CO_2 m^{-2} hr^{-1})
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
2
3
4
6
7
8
9
10
Week

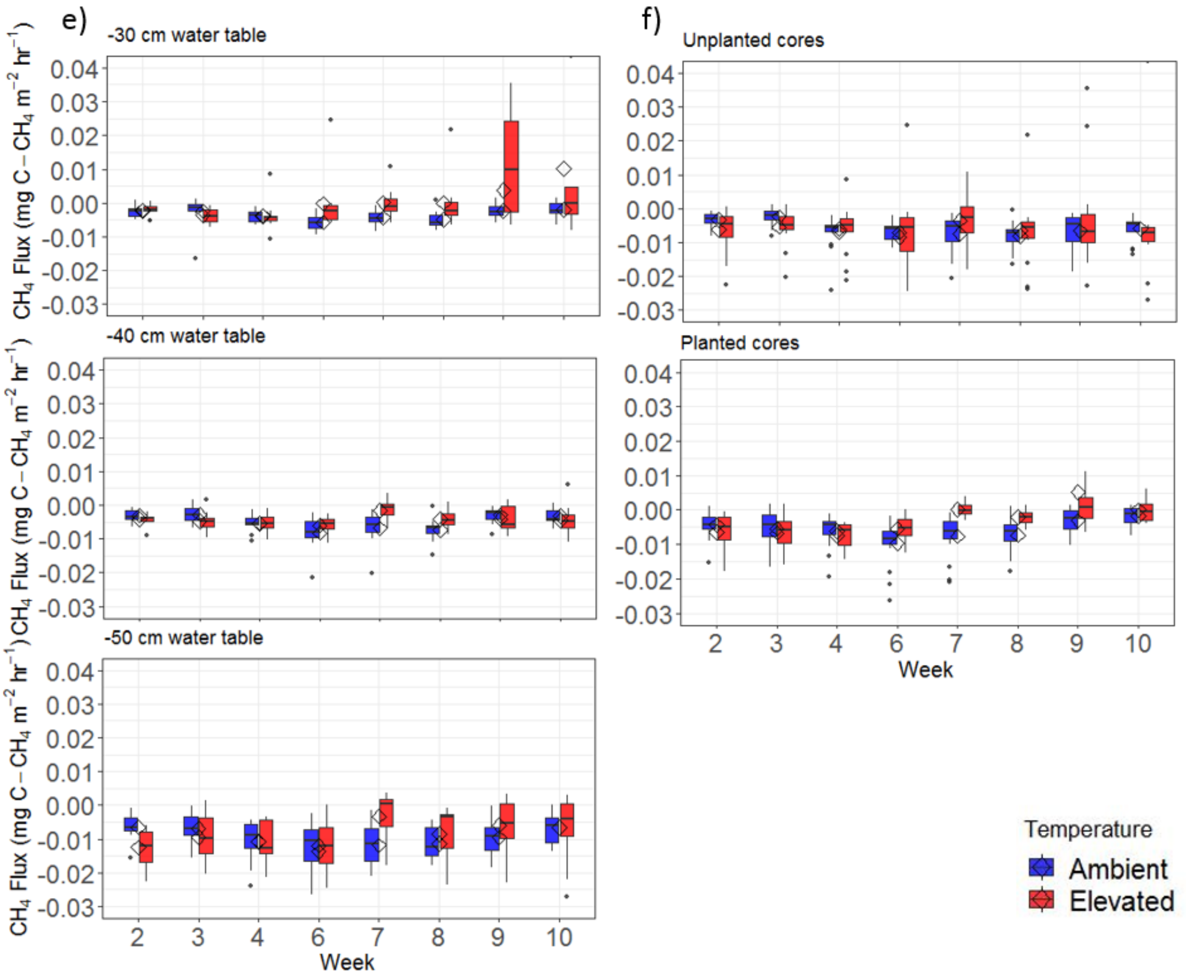


Figure 4.7: GHG emissions from peat cores at the three water table levels (-30 cm, -40 cm and -50 cm). Values are means from each week. Colours indicate: ambient (blue) and elevated (ambient +2°C) (red). a) Gross Primary Production (GPP); b) Soil respiration (Rh); c) Ecosystem respiration (ER); d) Net Ecosystem Exchange (NEE); e) Methane flux (CH_4) from the three water table levels; f) Methane flux (CH_4) from planted and unplanted cores. Some outliers were removed from CH_4 graphs to fit the data to a fixed scale.

Consumption dominated the CH_4 fluxes while CH_4 emissions were only detected in 11% of all samples. The rate of CH_4 consumption was one third higher from the ambient temperature treatment as compared to the elevated temperature treatment and significantly higher (by 50%)

in the unplanted cores than in the planted cores (Table 4.3, Fig. 4.7). Methane oxidation was 40% higher at the -50 cm than at the -40 cm water level, and 75% higher at the -50 cm than at the -30 cm, and these differences were all statistically significant (Table 4.4, Fig. 4.7). There were no statistically significant interactions between any of the dependent variables.

The DOC concentration in peat pore water and drainage water was not affected by temperature, however, it was higher in planted cores (in pore water – by 23%, in drainage water – by 19%) (Fig. 4.8, Table 4.5). Raising the water table resulted in increased DOC concentrations in the -40 cm (in pore water - by 34%, in drainage water by 31%) and -30 cm (in pore water – by 31% and in drainage water – by 40%) treatments compared to the -50 cm water level (Fig. 4.8, Table 4.6). There was a statistically significant interaction between planting and temperature in the pore water DOC, and between water table and temperature in the drainage water DOC (Fig 4.8, Table 4.5). The presence of these interactions may explain the borderline P-values for the temperature treatment in the pore and drainage samples: the effect of warming on DOC concentrations was confined only to a subset of samples. The similar responses of both the pore and the drainage water DOC to the three factors (planting, temperature and water table) (Table 4.5) show that using the drainage water is a good predictor of processes which affect DOC production and consumption in the top 10 cm of soil. The DOC concentration values in molar units are presented in Table 4.7.

	df	χ2	P-value
DOC - R			
Temperature	1	3.81	0.051
Planting	1	20.75	**<0.001 *****
Water table	2	25.6	**<0.001 *****
Water table:Temperature	2	1.34	0.511
Water table:Planting	2	1.96	0.375
Planting:Temperature	1	6.41	**0.011***
DOC - D			
Temperature	1	3.43	0.064
Planting	1	8.35	**0.004 ****
Water table	2	10.98	**0.004 ****
Water table:Temperature	2	6.26	**0.044 ***
Water table:Planting	2	3.54	0.17
Planting:Temperature	1	1.06	0.304

Table 4.5: Effects of temperature, water table position and cropping treatments and their interactions on DOC in topsoil water (R) and drainage water (D). The analysis was done with linear mixed model (lmer) (which included ‘week’ and ‘core’ as random effects, to take into account the temporal and spatial pseudoreplication). The total number of D samples was n=127 (two collection campaigns) and the R samples was n=250 (four collection campaigns).

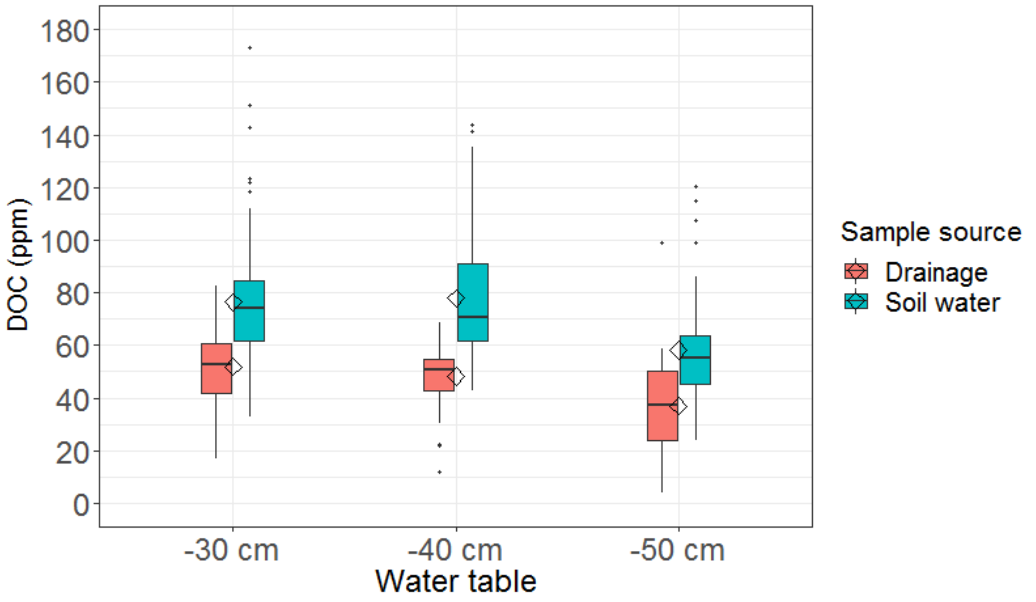
	z-value	P-value
DOC - R		
WT (-30 cm) & WT (-40 cm)	0.26	0.963
WT (-30 cm) & WT (-50 cm)	-4.56	**<0.001 *****
WT (-40 cm) & WT (-50 cm)	-4.83	**<0.001 *****
DOC - D		
WT (-30 cm) & WT (-40 cm)	-0.4	0.914
WT (-30 cm) & WT (-50 cm)	-3.11	**0.005 ****
WT (-40 cm) & WT (-50 cm)	-2.68	**0.02 ***

Table 4.6: Post hoc Tukey test of effect of water table levels on DOC collected from topsoil water (R) and drainage water (D). Displayed are z-values and P-values of the test.

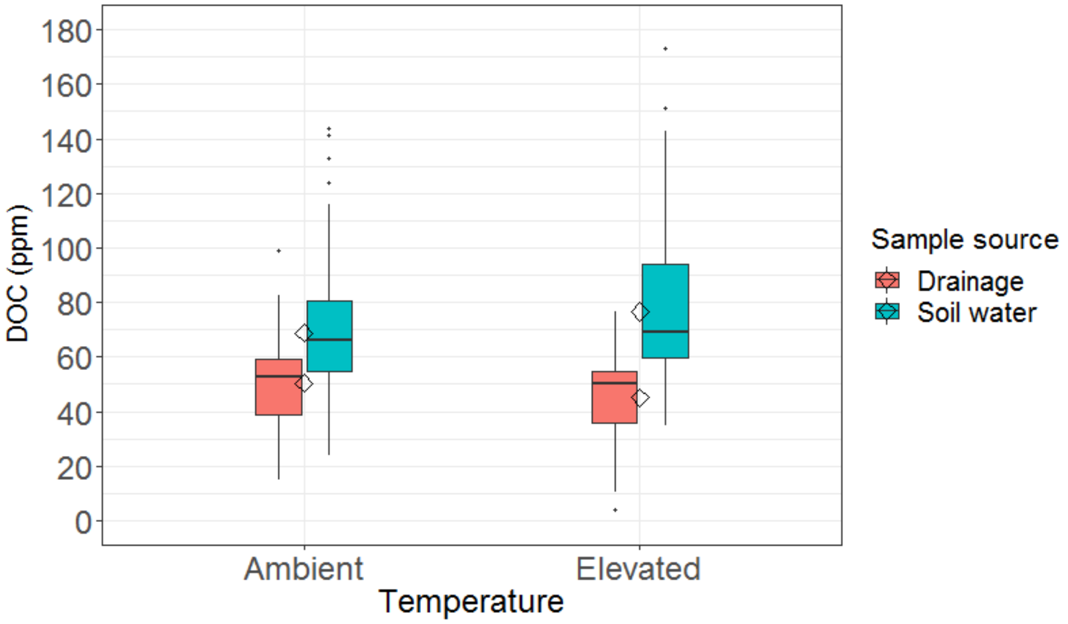
	Pore water	**Drainage water**
A30P	5.66	3.98
A30U	6.04	4.29
A40P	6.89	4.51
A40U	5.56	4.62
A50P	5.28	3.32
A50U	4.25	4.5
E30P	7.75	4.17
E30U	5.83	4.72
E40P	7.58	3.39
E40U	5.85	4.21
E50P	5.86	1.93
E50U	3.7	3.61

Table 4.7: Mean DOC values from all treatment combinations in mmol/l. A30P – ambient -30 cm planted, A30U – ambient -30 cm not planted, A40P – ambient -40 cm planted, A40U – ambient -40 cm not planted, A50P – ambient -50 cm planted, A50U – ambient -50 cm not planted, E30P – +2°C -30 cm planted, E30U – +2°C -30 cm not planted, E40P – +2°C -40 cm planted, E40U – +2°C -40 cm not planted, E50P – +2°C -50 cm planted, E50U – +2°C -50 cm not planted.

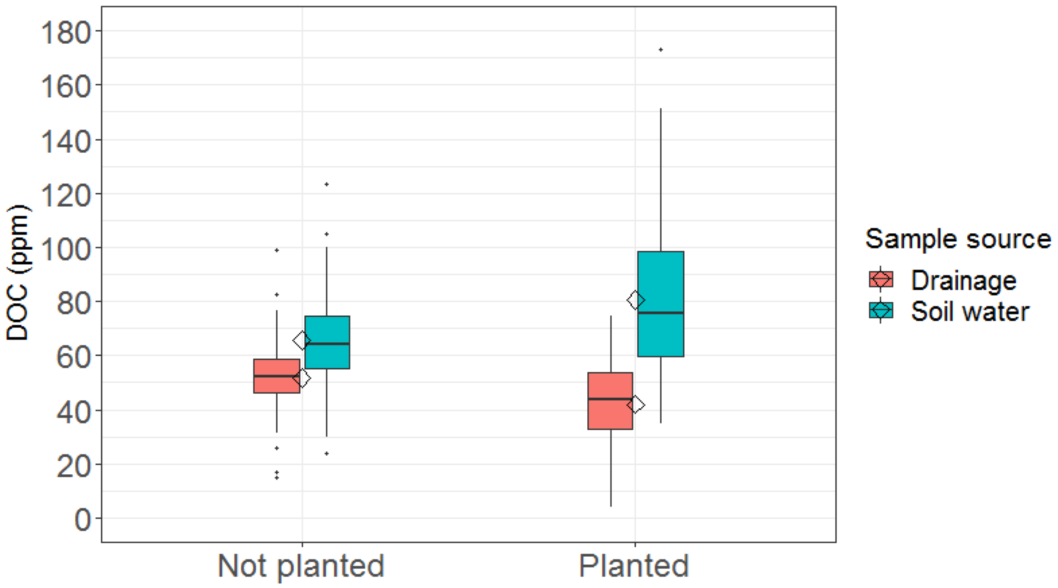
a)


DOC (ppm)
180
160
140
120
100
80
60
40
20
0
-30 cm
-40 cm
-50 cm
Water table
Sample source
Drainage
Soil water

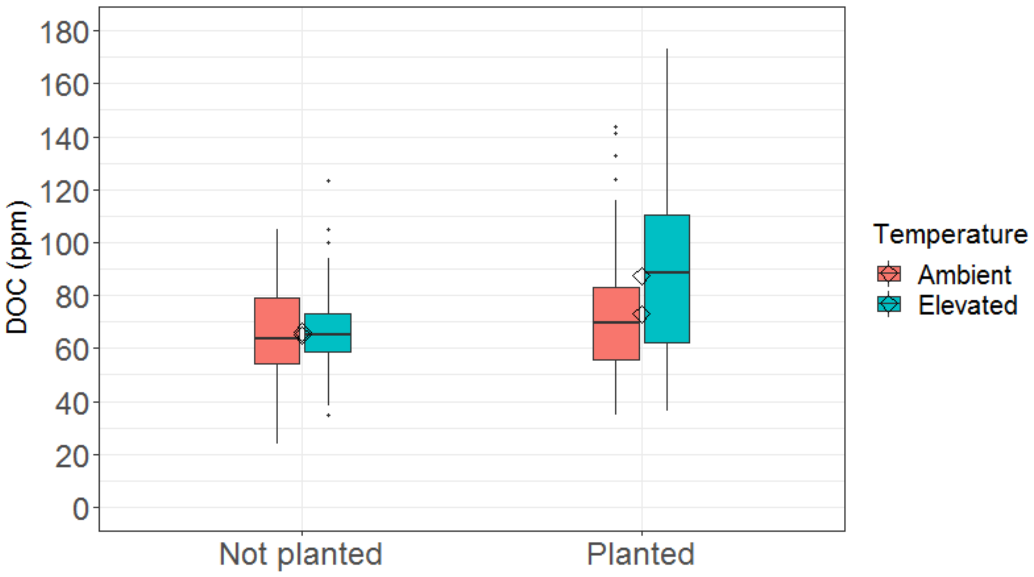
b)


DOC (ppm)
180
160
140
120
100
80
60
40
20
0
Ambient
Elevated
Temperature
Sample source
Drainage
Soil water

c)


DOC (ppm)
180
160
140
120
100
80
60
40
20
0
Not planted
Planted
Sample source
Drainage
Soil water

d)


DOC (ppm)
180
160
140
120
100
80
60
40
20
0
Not planted
Planted
Temperature
Ambient
Elevated

e)

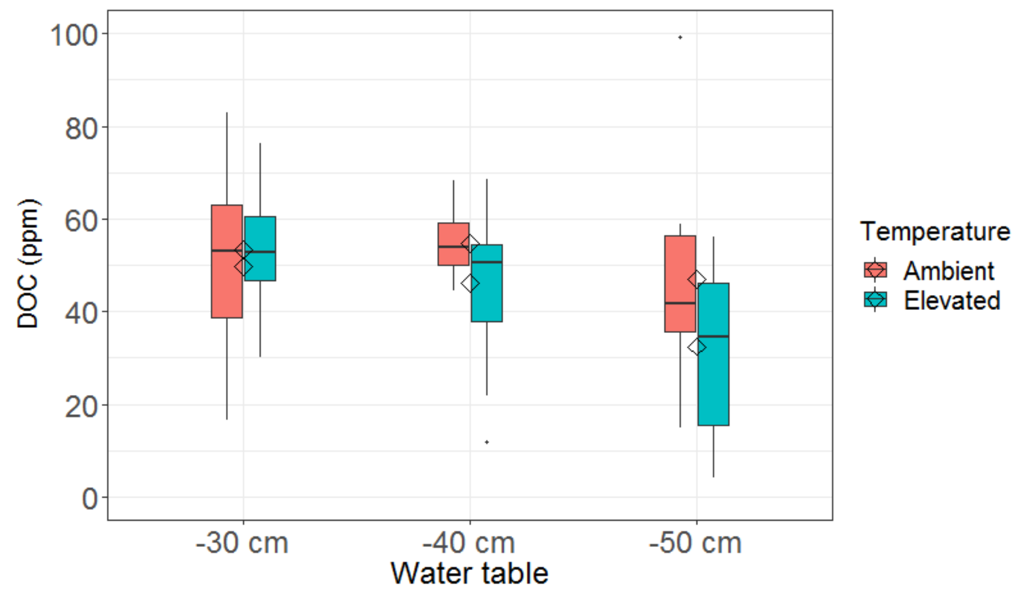


Figure 4.8: Mean DOC concentrations in pore and drainage water from: a) three water table treatments (-30 cm, -40 cm and -50 cm); b) two temperature treatments (ambient and ambient +2°C); c) two cropping treatments (planted and fallow). Interactions between variables: d) DOC concentrations in pore water samples by temperature and cropping status; e) DOC concentrations in drainage water samples by temperature and water table.

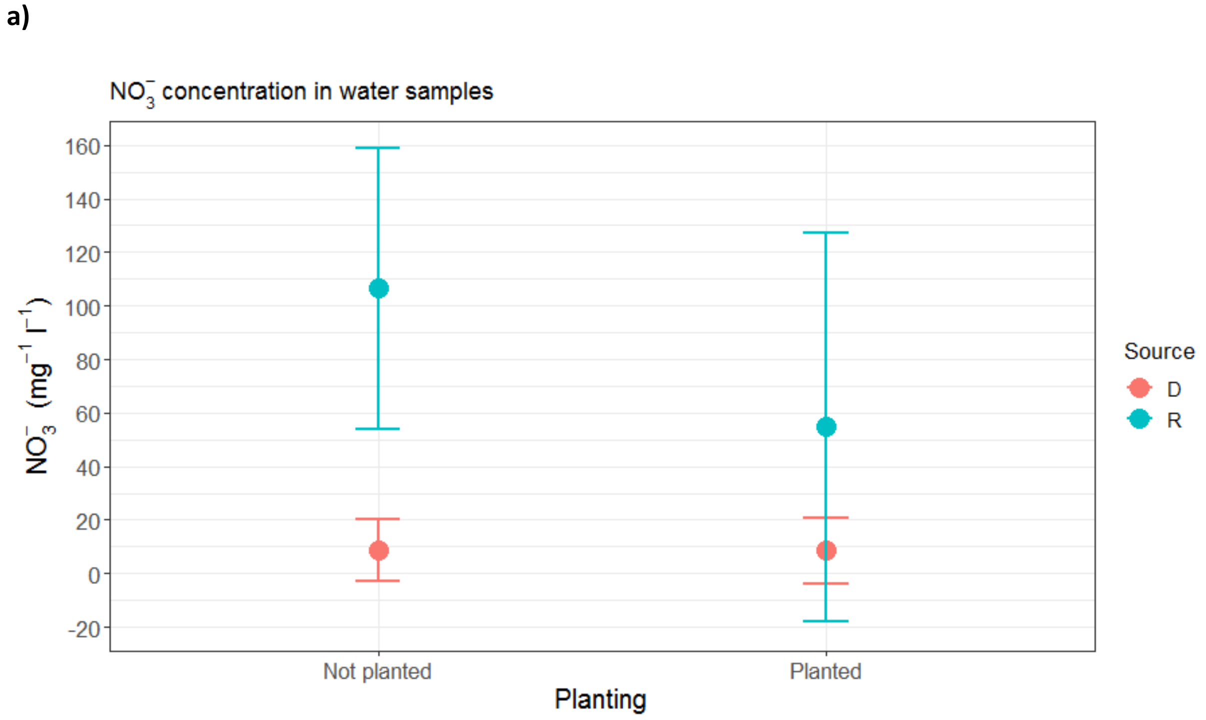
Pore water NO_3^- concentrations were significantly lower in the elevated temperature treatment and in the unplanted cores (Table 4.8, Fig. 4.9). They were significantly lower in the -30 cm and -40 cm water table treatments when compared with the -50 cm water table, however, there was no significant difference between the -30 cm and -40 cm treatments (Table 4.9, Fig. 4.9). There were significant interactions in pore water NO_3^- content between the cropping status and the water table level and between the cropping status and the temperature: the difference in the average NO_3^- concentration between the planted and the unplanted cores was lowered with a decreasing water table and increasing the temperature lowered the concentration in planted cores more severely. Nitrate collected from the drainage was lower in the elevated temperature treatment, however, neither the water table nor the crop presence had any statistically significant effect on NO_3^- concentrations (Table 4.8, Fig. 4.9). Ammonium collected from the pore water was significantly higher in the elevated temperature treatment (Table 4.8, Fig. 4.9). Neither the crop presence nor the water table had any significant effect on NH_4^+ content in the pore water (Table 4.8, Fig. 4.10). There was an interaction between the water table and the temperature: whereas NH_4^+ concentration in the pore water increased with a raising water table in the ambient temperature treatment, there was no such a relationship in the elevated temperature treatment. Ammonium concentrations in the drainage water were significantly higher in the ambient temperature and significantly higher in the -30 cm water table as compared to the -40 cm and -50 cm water table depths (Table 4.9, Fig. 4.10). The presence of romaine lettuce had no effect on NH_4^+ concentrations in the drainage water (Table 4.8, Fig. 4.10). There was a significant positive relationship between Rh and CH_4 emissions and NH_4^+ and NO_3^- concentrations in both the pore water and the drainage samples.

	lmer			lm		
NO_3^-- R	**df**	**χ2**	**P-value**	**df**	**F-value**	**P-value**
Planting	1	1538.6	**<0.001 *****	1, 52	70.51	**<0.001 *****
Temperature	1	1501.5	**<0.001 *****	1, 52	10.14	**0.002 ****
Water.table	2	1540.8	**<0.001 *****	2, 52	34.29	**<0.001 *****
Water table:*Temperature	2	2.44	0.296	2, 52	0.82	0.444
Temperature*Planting	1	5.51	**0.019 ***	1, 52	4.62	**0.036 ***
Water.table*Planting	2	8.92	**0.012 ***	2, 52	4.97	**0.011 ***
NH_4^+- R						
Planting	1	0.28	0.596	1, 52	0.54	0.467
Temperature	1	5.61	**0.018 ***	1, 52	7.23	**0.01 ***
Water.table	2	2.02	0.365	2, 52	1.95	0.152
Water table:*Temperature	2	12.26	**0.002 ****	2, 52	5.58	**0.006 ****
Temperature*Planting	1	0.43	0.51	1, 52	0.2	0.654
Water.table*Planting	2	0.38	0.828	2, 52	0.2	0.82
NO_3^-- D						
Planting	-	-	-	1, 50	0.99	0.323
Temperature	-	-	-	1, 50	7.33	**0.009 ****
Water.table	-	-	-	2, 50	0.75	0.48
Water table:*Temperature	-	-	-	2, 50	0.63	0.536
Temperature*Planting	-	-	-	1, 50	0.59	0.447
Water.table*Planting	-	-	-	2, 50	1.63	0.207
NH_4^+- D						
Planting	-	-	-	1, 50	0	0.998
Temperature	-	-	-	1, 50	27.13	**<0.001 *****
Water.table	-	-	-	2, 50	88.35	**<0.001 *****
Water table:*Temperature	-	-	-	2, 50	1.56	0.221
Temperature*Planting	-	-	-	1, 50	0.37	0.545
Water.table*Planting	-	-	-	2, 50	0.27	0.768

Table 4.8: Effects of temperature, water table position and cropping treatments and their interactions on concentrations of NO_3^- and NH_4^+ in pore water (R) and drainage water (D).

	t-value	**P-value**
NO_3^-- R		
WT (-30 cm) & WT (-40 cm)	1.22	0.447
WT (-30 cm) & WT (-50 cm)	5.52	**<0.001 *****
WT (-40 cm) & WT (-50 cm)	4.18	**<0.001 *****
NO_3^-- D		
WT (-30 cm) & WT (-40 cm)	-0.14	0.989
WT (-30 cm) & WT (-50 cm)	0.417	0.909
WT (-40 cm) & WT (-50 cm)	0.548	0.848
NH_4^+- D		
WT (-30 cm) & WT (-40 cm)	-7.35	**<0.001 *****
WT (-30 cm) & WT (-50 cm)	-9.809	**<0.001 *****
WT (-40 cm) & WT (-50 cm)	-2.24	0.074

Table 4.9: Post hoc Tukey test of effect of water table levels on NO_3^- and NH_4^+ collected from pore water (R) and drainage water (D).



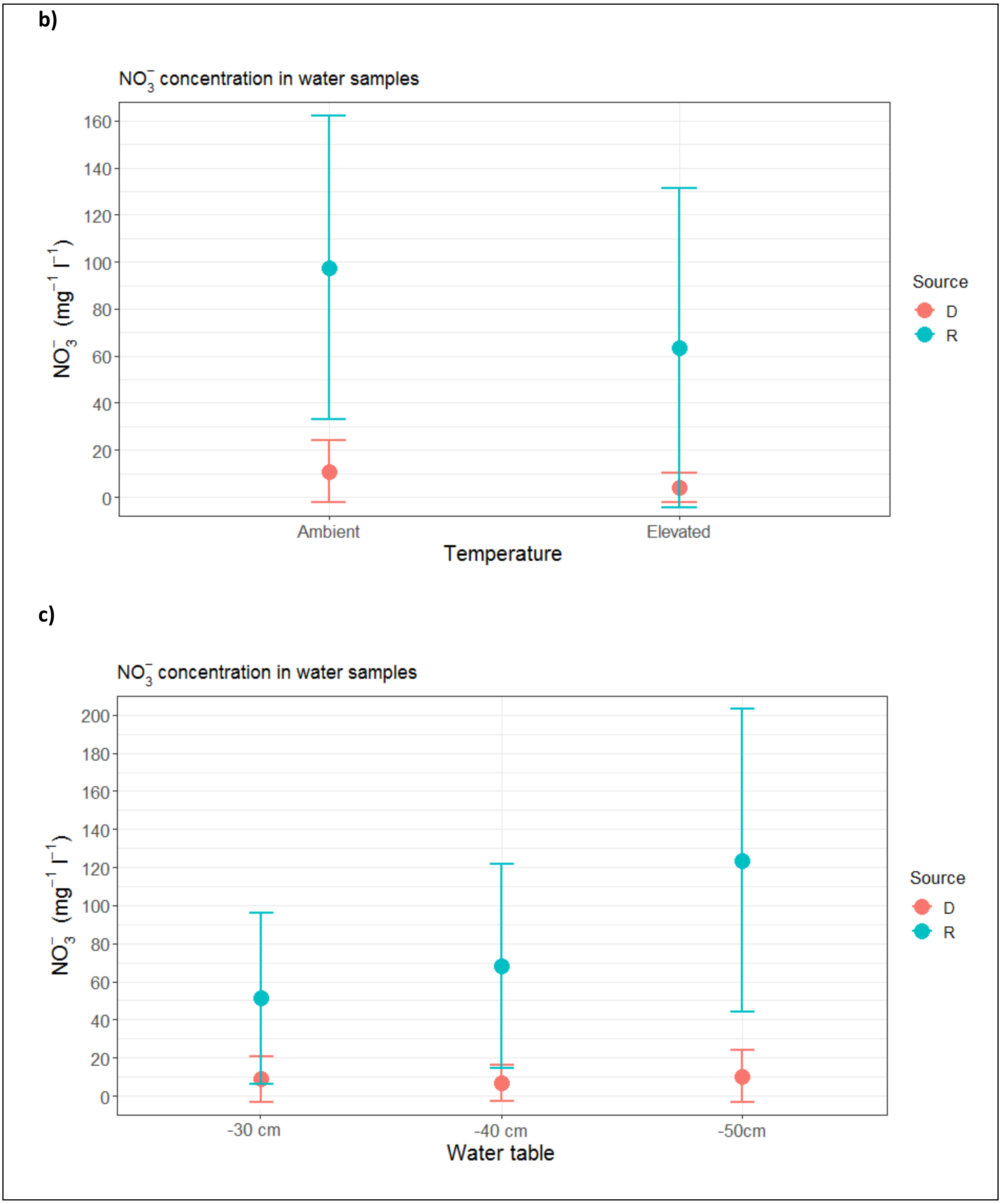
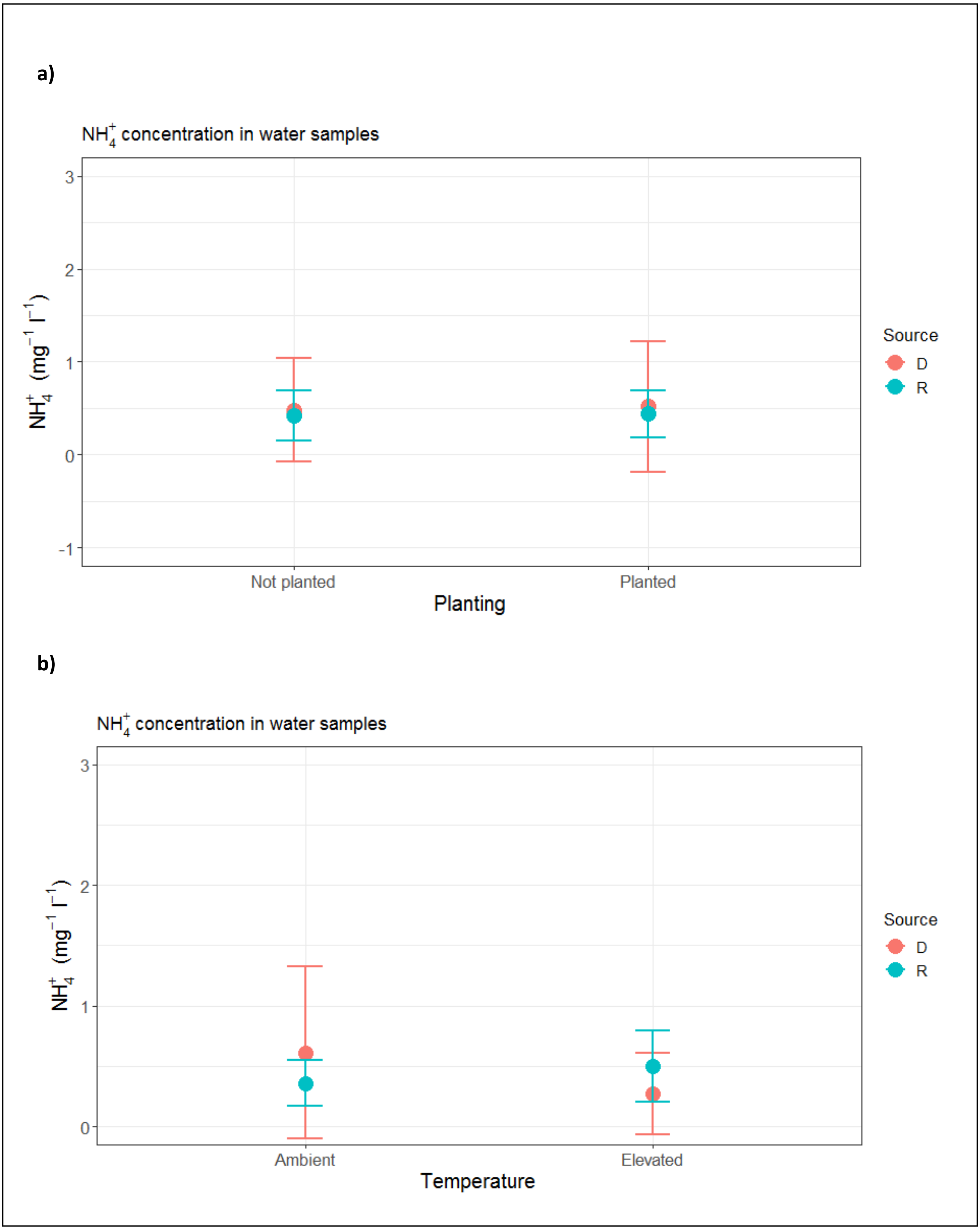


Figure 4.9: Concentration of NO_3^- in pore (R) and drainage (D) water in a) planted and fallow cores; b) ambient and ambient + 2°C cores; c) in three water table depths (-30 cm, -40 cm and -50 cm).


a)
NH_4^+ concentration in water samples
NH_4^+ (mg^{-1} l^{-1})
3
2
1
0
-1
Not planted
Planted
Planting
Source
● D
● R
b)
NH_4^+ concentration in water samples
NH_4^+ (mg^{-1} l^{-1})
3
2
1
0
Ambient
Elevated
Temperature
Source
● D
● R

c)

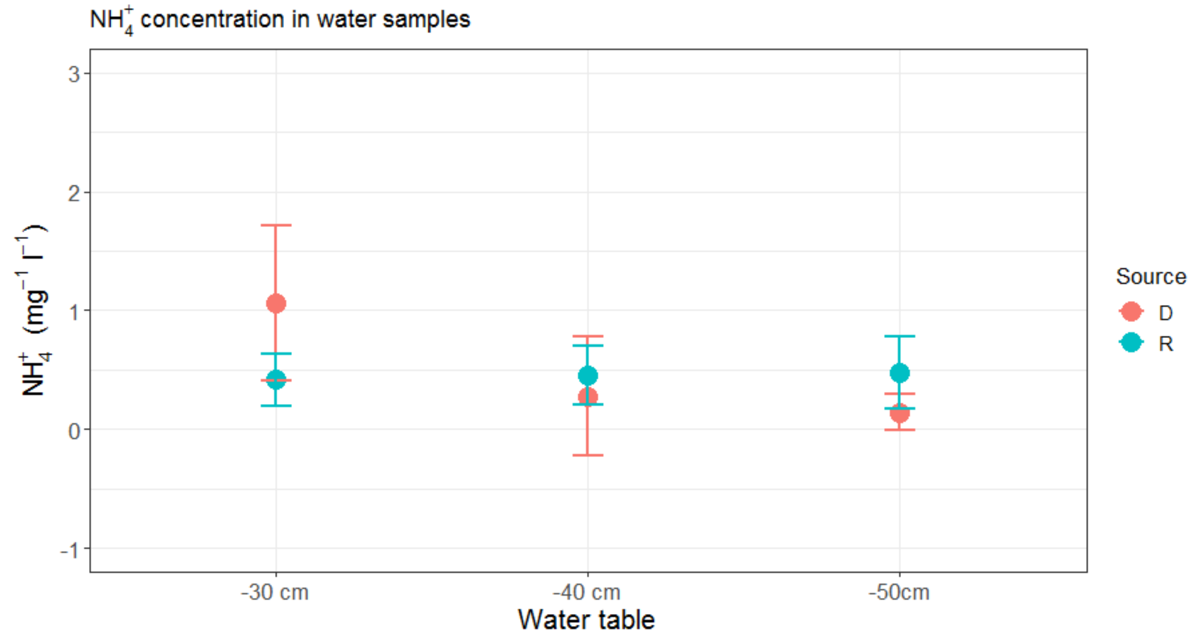


Figure 4.10: Concentration of NH$_4^+$ in pore (R) and drainage (D) water in a) planted and fallow cores; b) ambient and ambient + 2°C cores; c) in three water table depths (-30 cm, -40 cm and -50 cm).

4.4 Discussion

4.4.1 Romaine lettuce yield

The reduced romaine lettuce fresh and dry biomass production in the -30 cm water level treatment compared to the -50 cm water level is consistent with our previous study on celery (Matysek et al., 2019), but the romaine lettuce showed a more drastic loss of yield (32% decrease compared to 19% for celery). This probably reflects a greater sensitivity of romaine lettuce to waterlogged soil. Excessive soil water content leads to root hypoxia, which reduces stomatal conductance and photosynthetic rate (Neumann 1991; Yordanova 2005; Rood et al., 2010). In this experiment, only fresh, not dry, romaine lettuce biomass differed significantly between the -40 cm and the -50 cm treatments. This indicates that romaine lettuce growing at -

40 cm water level produced as much dry biomass as plants at the -50 cm water level, however, absorbed and stored less water. The Rh at the -40 cm water level was significantly lower than at the -50 cm water level, suggesting that this water level might be a good compromise to reduce peat wastage. Still, the fresh biomass was lower by one-fifth in the -40 cm water level than in the -50 cm, and this might influence the farmer to choose a deeper water level.

The weight of dried roots differed between the -40 cm and -50 cm treatments: in the soil layer between -10 cm and -30 cm and below -30 cm, root biomass was lower in the -40 cm water table treatment when compared to the -50 cm treatment, consistent with the physiological requirement for greater root mass to reach a deeper water table. Shifts in aboveground biomass production may be related to changes in root biomass as nutrient demand of shoots leads to expansion of the rooting system and, conversely, greater root biomass requires more photosynthate to sustain it (Murphy et al., 2009; Murphy and Moore, 2010). However, in our study total root biomass did not differ significantly between the -40 cm and -50 cm treatments, even though root biomass was lower in the soil layer below -30 cm in the -40 cm treatment when compared to the -50 cm treatment. The lower root biomass in the -40 cm water table treatment in the soil layer between -30 and -40 cm could be a possible result of hypoxia stress as upward capillary flow of water occurs, which limits root uptake of nutrients (Matsuo et al., 2017). A higher water table might therefore influence the total allocation of substrate and negatively affect also leaf biomass. Total root biomass significantly differed between -30 cm and -50 cm and corresponded to lower leaf dry and fresh biomass between the two treatments. It is likely that the decrease in root biomass was driven by limited root penetration due to the presence of a higher water level, since root presence below -30 cm was negligible in the -30 cm treatment. Greater root production may result in higher aboveground biomass due to greater access to nutrients (Itoh et al., 2009; Wang et al., 2015), although grain yield may not always be related to root length or rooting depth, especially in irrigated systems, in which crops do not need to develop an extensive rooting system in order to acquire water (Xue et al., 2003).

Our study showed that even a moderate temperature increase of 2°C can raise both fresh and dry leaf biomass. This is partially contrary to the results of our previous experiment on celery, in which a 5°C temperature increase did not affect the aboveground fresh weight and only increased the dry biomass. We hypothesized that +5°C temperature increase caused more intense water loss through stomata, and, consequently, a lower fresh weight in celery. This was not evident in the romaine lettuce as the growth temperature was lower than in the celery experiment. Stomatal conductance increases when temperature rises, as long as there is no drought stress and the temperature value does not pass a threshold above which photosynthesis is disrupted. This threshold is usually around 30°C for plants adapted to cold temperatures and above 40°C for those which typically grow in warmer conditions (Sage and Kubien 2007; Urban et al., 2017). Romaine lettuce is a crop with low heat tolerance, which manifests as bolting and shortening of the vegetative period when growing in temperatures higher than optimal, and it achieves best yields at 27-30°C (Dufault et al., 2009; Frantz et al., 2004). However, the temperatures used in our study were below this threshold, therefore warming of 2°C would not result in yield decline. In this study, a higher temperature under spring conditions clearly raised the rate of photosynthesis (as also seen from the GPP values) and positively affected biomass production. Warming may stimulate expansion of the rooting system (Batts et al., 1998; Hu et al., 2018) and fine root production (Yin et al., 2013): the resulting increased resource uptake can then enhance aboveground growth. In this experiment, higher total root mass in the elevated temperature treatment was largely driven by roots in the top 10 cm and there was no effect of higher temperature on root biomass below -30 cm depth. A similar outcome was described by Arndal et al. (2018): more root production in the topsoil (top 8 cm), but less fine roots and less root biomass deeper in the profile. Ma et al. (2017): noted higher root biomass in the 0-10 cm layer on a steppe following 4°C warming. Greater root production in the topsoil could improve fertilizer use efficiency, increasing aboveground biomass.

Supply of photosynthate is one of the factors determining biomass partitioning: investment in one sink (for example, in either roots or shoots) may come at the expense of the other (Minchin et al., 1994; Radville et al., 2016). Agricultural studies show varying effects of warming on biomass partitioning between different sinks, pointing to physiological differences between crops. In the example of barley a reduction in photosynthate supply led to higher biomass accumulation in shoots and lesser in roots (Minchin et al., 1994). In wheat a 1-3°C warming of caused lower photosynthate partitioning to grain (Batts et al., 1998). Warming led to greater photosynthate allocation to lettuce roots as compared to shoots (He et al., 2009). However, it is also reported that warming could strengthen the shoot sink at the expense of roots: a temperature increase from 14°C to 22°C increased LAI in lettuce and had negative impact on root growth (Lorenz, 1980). Moreover, partitioning between different sinks can also show seasonal trends (Iversen, 2018). A 2°C warming in our study resulted in a higher whole-plant photosynthetic rate, however, the root: shoot ratio remained unchanged, signifying that neither sink was preferred over the other, possibly due ample supply of water, which removed the need for rooting system expansion. This outcome should be reassuring to the farmers, since it would suggest that the global warming will most likely not drain resources (fertilizer, soil nutrients) ‘in vain’, that is on crop parts with no commercial value (lettuce roots).

Lower water table levels are often found to increase the allocation of biomass to roots. On a temperate bog, lower water table conditions shifted carbohydrate allocation towards roots at the expense of shoots (Moorphy & Moore, 2010). Water stress increased the root:shoot ratio in soybean (He et al., 2017). Shoots of *Carex* sedges accumulated more biomass than roots in a high water level (0 cm) as compared to when the water table was low (-15 cm) (Li et al., 2017). In our experiment raising the water table did not affect the root:shoot ratio.

4.4.2 Emissions of greenhouse gases

A higher Rh (by 40%) in the -50 cm water level than in the -40 cm indicates that increasing the water table by just 10 cm from the field level is a viable option for peat preservation. The lower Rh with the shallower water level is related to the lower unsaturated peat volume available for aerobic decomposition. High water content in peat diminishes diffusion of oxygen, therefore hampering activity of aerobic decomposers (Wickland and Neff, 2008; Taft et al., 2017). The lack of a significant difference in Rh between the -30 cm and -40 cm water levels suggest that soil C decomposition in the shallower soil layer is more advanced than deeper in the soil. In agreement with this interpretation, Kechavarzi et al. (2007) reports that reducing the water table from 0 cm to -30 cm resulted in a CO_2 flux emission increase that was less than the increase that was observed when decreasing the water level from -30 cm to -50 cm. This supports the hypothesis that decomposition of deeper peat soil layers are more sensitive to changes in water conditions and so manipulating the water table at the level found in the field (-50 cm) to -40 cm might help to reduce peat mineralization. The lack of a significant difference in GPP between water table levels might suggest that the crop accumulated as much C at all water levels. This is not reflected in the leaf biomass data, which shows that the water table position had a significant effect on dry and fresh leaf weight, and we infer that although raising the water table reduces the rate of peat decomposition, there is no net increase total C accumulation in the ecosystem.

The higher Rh in the elevated temperature treatment showed that even a 2°C increase in temperature can stimulate peat C losses. Temperature increases enhance Rh by increasing the metabolism of organic matter decomposer microbes (Ziegler et al., 2013), but also by greater oxygen presence in soil as higher temperatures cause greater evaporation, less water content and a lower diffusion barrier to O_2, which leads to great O_2 ingress and proliferation of aerobic microorganisms (Gill et al., 2017). In this study soil water content in the top soil did differ significantly between the two temperature treatments (being 8% in the elevated temperature treatment). NEE and GPP increasing with increased temperature suggests that warming increased the sink strength of romaine lettuce as more C was sequestered, despite increases in Rh and ER.

Plants influence CH_4 flux by modifying consumption and production of CH_4, as well as its transport in the case of species with an aerenchyma (an air space in tissue, which facilitates gaseous transportation between organs), allowing CH_4 to bypass the shallower aerobic soil layer, and voiding CH_4 oxidation (Koelbener et al., 2010). However, given that romaine lettuce does not have aerenchyma, this process is not relevant in this case. On the other hand, higher CH_4 consumption from unplanted cores indicates that the presence of romaine lettuce has an influence on CH_4 fluxes, either by increasing CH_4 production or reducing CH_4 consumption. Even though soil water content was lower in planted cores it did not result in higher rates of CH_4 consumption. Studies on agricultural peatlands suggest that CH_4 emissions rates are not consistent in different types of crops (Norberg et al., 2016), although bare soils are typically associated with lower CH_4 uptake than soils where crops are grown (Maljanen et al., 2004). This is related to the presence of roots which modify communities of methanotrophs and methanogens, for instance by secretion of root exudates, which may stimulate or impede microbial activity (Koelbener et al., 2010; Girkin et al., 2018) and by provision of carbon substrate that is readily-available for decomposition (Watson et al., 1997; Laanbroek, 2010). Root exudates provide labile substrates which microbial communities (both methanotrophic and methanogenic) use as nutrients as well as inhibitors, which slow down decomposition (Girkin et al., 2018). It could by hypothesized that in this study romaine root secretions played an important part in enhancing CH_4 production as labile root-derived organic substrates were decomposed by fermenting bacteria into products which were then used by methanogenic archaea (Segers, 1998; Serrano-Silva et al., 2014; Girkin et al., 2018). This hypothesis is supported by higher DOC content in soil pore water of planted cores.

In this study, CH_4 oxidation dominated in all water table levels, despite high water saturation values (Fig. 4.6), especially from the -30 cm water table treatment. The dominance of CH_4 consumption over production in all treatments in this experiment is expected as research shows that a water table of -30 cm to -40 cm could be enough for full oxidation to occur in cultivated peats (Nykanen et al., 1995; Karki et al., 2016; Poyda 2016;). This is attributable to the high potential of oxygen to penetrate down the soil profile; e.g. Thomas et al. (1995) noted that oxygen was present in peat cores at -5 cm depth when the water table was kept within 1 cm to the surface, whereas McDonald et al. (1996) detected CH_4 oxidation at -30 cm in a peat core when the water table was at the surface. These studies are consistent with the results of this experiment where even the highest water table of -30 cm promoted CH_4 consumption over production. The -30 cm and -40 cm water level treatments had similar soil moisture content at the -12 cm depth, and comparable CH_4 fluxes, which suggests that soil water content in the topsoil was the primary driver of CH_4 emissions. Once the water table is raised to a certain level, any further increase may not result in changes in topsoil soil water content, and consequently, there may be little effect on CH_4 fluxes (Rinne et al., 2007). Therefore, lowering the water table would not lead to more CH_4 being oxidised. As we hypothesized before, this water table level establishes an oxic layer that is sufficient to result in methanotroph dominance over methanogens (Juszczak et al., 2012).

The CH_4 consumption was lower in the elevated temperature treatment, which is unexpected given that warming is associated with drying of the upper soil layer (Curry, 2009). In other studies the temperature response of CH_4 emissions is complex and shows contradictory patterns: a 1°C increase in air temperature influenced CH_4 flux from organic soil, although the direction of the effect was season-dependent as warming increased CH_4 uptake early in the summer and decreased it later in the season (Pedersen et al., 2017); a 2-3°C warming was shown not to affect peat CH_4 emissions (Kim et al., 2012; Yang et al. 2014); drying of boreal fen had greater impact on reducing CH_4 flux than the increased temperature (Peltoniemi et al., 2016). D'imperio et al.

(2017) noted increased, though not to statistically significant degree, CH_4 uptake from dry Arctic soils with warming and this was associated with lower soil water content associated with the temperature increase. The results of the present study suggest that a decrease in peat moisture in the higher temperature treatment had little effect on the rate of CH_4 uptake. The lower rate of CH_4 oxidation in the elevated temperature could be due to higher sensitivity (and consequently enhanced activity) of methanogens (as compared to methanotrophs) to temperature increases (Das and Adhya, 2012; van Winden et al., 2012; Cui et al., 2015; Tveit et al., 2015; Pedersen et al., 2018; Sepulveda-Jauregui et al., 2018).

4.4.3 Production of DOC

The highest concentrations of DOC in peat soils are often found during periods of the most intense waterlogging (Chow et al., 2006; Frank et al., 2017). This could be explained by the highest content of easily decomposable organic matter being present close to the surface – and its easy leaching (Thibodeaux and Aguilar, 2005; Chow et al., 2006). However, soil water content and water table position have previously been found to have limited or no impact on DOC concentrations in peat, even when there was a clear link between water table depth and CO_2 emissions (Chow et al., 2006; Frank et al., 2017; Lundin et al., 2017). Nevertheless, many of the available studies analyse effects of peatland restoration by rewetting: these are conditions different from manipulating the water table in intensively cultivated peats.

In this experiment, increasing the water table level from the field level of -50 cm to -30 cm raised DOC concentration in topsoil pore water via increased soil water content, which led to greater release of C in pore water (Clark et al., 2009). Greater DOC presence in topsoil makes it vulnerable to removal into water bodies via flooding and into rivers connected to the drainage system. Moreover, DOC in pore water may be transported down the peat profile, which could stimulate further organic matter decomposition via the priming effect (Qiu et al., 2016; Morling et al., 2017). The lack of statistically significant differences in DOC content between the -30 cm and -40 cm treatments in both drainage and pore water samples supports our findings regarding CO_2 emissions which we report above: there is little difference in how water table levels above a certain threshold affect organic matter decomposition in the topsoil. What it means for C loss from agricultural peatlands is that raising the water table seasonally as a means of peat preservation would lead to greater DOC production and transportation into water bodies. This DOC will eventually degrade into CO_2, contributing to 'offsite emissions' of GHG (Moran and Zepp, 1997; Shen and Benner, 2018). It is estimated that CO_2 emissions from oxidising DOC constitute 2% of CO_2 emissions from agricultural peats in the UK (Evans et al., 2017).

Concentrations of DOC in soils and inland waters of the temperate zone show seasonal variations, highlighting the positive effect of temperature on DOC production (Miller et al., 2001; Lumsdon et al., 2005; Dawson et al., 2011). Nevertheless, warming may also result in decreases in soil water content, which in dry conditions limits the activity of microbial decomposers and, consequently, formation of DOC (Yu et al., 2014). In our study a 2°C warming had no effect on DOC values in both drainage and pore water. Similarly, Yu et al. (2014) found no effect of experimental warming of 1–1.4°C on DOC concentration in the topsoil of an alpine meadow and Chow et al. (2006) reported no difference in agricultural peat DOC content between temperature treatments of 10°C, 20°C and 30°C. Although, in this experiment the rates of organic matter decomposition were higher in the elevated temperature treatment (as proven by higher Rh rates), this did not translate into higher production of DOC. Even though the values of DOC were lower in drainage samples than in pore water, the uniform reactions of pore and drainage water to temperature and water table treatments shows that using the drainage water may be a good predictor of processes which affect DOC concentration in topsoil pore water.

In peat soils, production of DOC depends on the type of vegetation cover as well as presence or absence of plants (Banaś and Gos, 2004; Basiliko et al., 2012; Clay et al., 2012). Addition of organic matter from vegetation provides a pool from which DOC is produced and root exudates stimulate activity of decomposing microbes. However, there is much less known about DOC dynamics in agricultural peat: whether DOC production is related to the type of crop and to what extent it differs between fallow and cropping land uses. In the pore water samples the DOC concentration was higher in planted cores, which suggests that root exudates stimulated organic matter decomposition. Conversely, drainage samples contained lower DOC concentrations in planted cores: this can be explained by water absorption by plants, which decreased soil water content and consequently reduced DOC leaching into the drainage water.

The combination of elevated temperature and planting resulted in higher DOC concentrations in pore water. A similar outcome is reported by Harrison et al. (2008) and Fenner et al. (2007). The data on root biomass (increased dry root weight in the top 20 cm in the warmer treatment) suggests that increased temperature led to higher root production, which might have caused greater root exudate release and, consequently, exudate decay and increased rates of organic matter decomposition via priming (Basiliko et al., 2012; Leroy et al., 2017). For this reason, the predicted future 2°C warming by early next Century will likely contribute to higher DOC production and losses to water bodies from agriculturally-used fields of the Fens. The interaction between the water table and temperature in drainage samples shows that DOC values were similar in both the ambient and the elevated temperature at the water table of -30 cm, however, the fall in DOC content with decreasing water levels was much sharper in the elevated temperature treatment. This interaction may suggest that warming coupled with low water table levels could result in less DOC content in drainage waters, possibly due to dominance of another pathway of C loss: soil respiration.

We estimated annual C losses from the entire Fens area: the loss of C as DOC was much higher than the loss as CO_2 (Table 4.10). These estimates are based on the thermal and hydrological conditions of early summer we used in this experiment, therefore they overestimate the total loss of C, as the rate of decomposition is most certainly lower through autumn and winter. Nevertheless, they highlight the importance of DOC as an important contributor to global warming as 90% of ocean DOC will eventually oxidise to CO_2 (IPCC, 2014b).

Treatment	Mt C-DOC	Mt C-CO_2	C-DOC as % of C-CO_2
A30P	0.08	-	-
E30P	0.11	-	-
A40P	0.1	-	-
E40P	0.11	-	-
A50P	0.08	-	-
E50P	0.09	-	-
A30U	0.09	0.7	12.59
E30U	0.09	1.18	7.26
A40U	0.09	1.23	6.63
E40U	0.09	1.61	5.34
A50U	0.06	2.26	2.76
E50U	0.05	2.61	2.08

Table 4.10: Total annual loss of C as CO_2 and DOC from the Fens area (3884.982 km^2). Carbon loss values are based on late spring/early summer temperature conditions of the experiment. The DOC estimates are based on the pore water DOC readings. The CO_2 emissions are based on reading from cores from the fallow treatment. The total annual discharge from the Fens was extrapolated from the annual discharge value for Baker's Fen: a rewetted cropland peat site in the Fens (Peacock et al., 2019). A30P – ambient -30 cm planted, A30U – ambient -30 cm not planted, A40P – ambient -40 cm planted, A40U – ambient -40 cm not planted, A50P – ambient -50 cm planted, A50U – ambient -50 cm not planted, E30P – +2°C -30 cm planted, E30U – +2°C -30 cm not planted, E40P – +2°C -40 cm planted, E40U – +2°C -40 cm not planted, E50P – +2°C -50 cm planted, E50U – +2°C -50 cm not planted.

4.4.4 Concentrations of NH_4^+ and NO_3^- in peat water

Conditions of water saturation in soil increase the rate of denitrification (transformation of NO_3^- into N_2O, NO and N_2) (Koops et al., 1996; van Beek et al., 2004; Amha and Bohne, 2011). Organic matter is firstly transformed to NH_4^+ ions, which are then transformed into NO_3^- by nitrifying bacteria. Nitrate ions are in the form of solution and therefore are prone to leaching (Hay and Porter, 2006). Peatland rewetting is reported to result in increases in soil NH_4^+ concentrations and decreases in NO_3^- content and to cause an overall decline in the presence of inorganic N (Lundin et al., 2017). Following peatland drainage, outflows of inorganic N are often reported to increase as peat starts to decompose and oxidising conditions begin to prevail (Lundin et al., 2017). In our experiment, NO_3^- content in the top soil fell with the rising water table, indicating that manipulating the water table at depth (-30 cm to -50 cm) had an impact on the rate of denitrification in the whole soil profile by affecting soil water content. The top soil layer is the most active zone for denitrification (Koops et al., 1996), therefore, raising the water table by 10 cm or more would potentially require more fertilizer input.

Other studies showed that warming of as little as 1°C (Munir et al., 2016) or 2.6°C (Chen et al., 2017) increased rates of nitrification and denitrification in soil. In our experiment raising the air temperature by 2°C lowered the concentrations of NH_4^+ and NO_3^- in the pore water, possibly by accelerating the breakdown of NH_4^+ and NO_3^- and increasing their rate of uptake by romaine lettuce roots. The interaction effect between the temperature and the plant presence indicated that NO_3^- loss from the pore water was enhanced in the planted elevated temperature cores. This could be explained by the higher root production in the elevated temperature treatment: root exudates are consumed by N-transforming bacteria (Zhang et al., 2016), hence higher root production would lead to accelerated denitrification rates in soil. The lack of effect of the crop presence on the drainage water concentrations of NH_4^+ and NO_3^- indicates that the roots of romaine lettuce absorbed only a fraction of all available N in the peat core. For this reason, raising the water table will require higher fertilizer inputs.

4.4.5 Carbon balance

The estimates of the annual C loss from the Fens are presented in Table 4.11. It has to be stressed that these figures are overestimated for reasons outlined in section 4.4.3. It should also be noted that the values represent only the fallow treatment (CO_2 uptake by the crop is not incorporated) to illustrate the scale of peat degradation through agricultural practices, rather than provide an accurate C footprint arising from the cultivation of the area.

It can be seen that the DOC flux did not significantly add to the total C loss or change the pattern observed in the CO_2 emissions: higher soil respiration in the elevated temperature and with the decreasing water table. Likewise, the effect of the CH_4 addition on the overall C loss was miniscule, as seen when comparing Table 4.10 and Table 4.11. It is worth noting that the mean CH_4 flux was predominately negative (uptake from the atmosphere), with the exception of the two elevated temperature -30 cm treatments. The finding of the most interest to farmers of the Fens should be the observation that raising the water table from the level currently applied (-50 cm) to -30 cm would result in an annual C loss that is three times lower.

Treatment	C-CH_4 mg m^{-2} hr^{-1}	C-CO_{2eq} (C-CH_4 + C-CO_2) g m^{-2} hr^{-1}	C-CO_{2eq} (C-CH_4 + C-CO_2) Mt yr^{-1}	C-CO_{2eq} (C-CH_4 + C-CO_2 + C-DOC) Mt yr^{-1}
A30P	-0,002	-	-	-
E30P	0,001	-	-	-
A40P	-0,006	-	-	-
E40P	-0,003	-	-	-
A50P	-0,009	-	-	-
E50P	-0,005	-	-	-
A30U	-0,004	0,02	0,70	0,78
E30U	0	0,03	1,18	1,26
A40U	-0,004	0,04	1,23	1,30
E40U	-0,005	0,05	1,60	1,68
A50U	-0,011	0,07	2,25	2,31
E50U	-0,013	0,08	2,60	2,65

Table 4.11: Total C loss to the atmosphere from the Fens area in C-CO_{2eq} (equivalents). The C-CO_{2eq} of C-CH_4 was obtained by multiplication by 28 (the Global Warming Potential of CH_4 over the period of 100 years) (IPCC, 2014c). The DOC estimates are based on the pore water DOC readings. The CO_2 emissions are based on reading from cores from the fallow treatment. The treatment abbreviations are the same as in Table 4.10. The methodology of C-DOC production estimation is described in Table 4.10. 90% of DOC entering oceans is expected to be oxidised into CO_2 (IPCC, 2014b) and this is reflected in the cumulative C-CO_{2eq} values.

4.5 Conclusion

The findings of this study indicate that climatic warming of 2°C would increase romaine lettuce yields as well as root biomass, pointing to the important role played by roots in nutrient acquisition. Raising the water table from -50 cm to -40 cm would decrease yield by one-fifth, which could be caused by limited nutrient extraction from the deeper peat layers and waterlogging injury. Increasing the water table from the field level to -40 cm was shown to reduce CO_2 emissions, while keeping CH_4 fluxes negative (oxidation), at the same time creating conditions that facilitate greater leaching of DOC. Warming of 2°C would inevitably lead to higher rates of peat decomposition and loss of C as CO_2 and DOC, however, more C would also be sequestered in the romaine lettuce crop. This temperature increase could offset C losses as CO_2, since the rise in soil respiration (18%) is lower than the increase in GPP (one-third), however, the final C balance would depend on the spacing of the crop in field and the duration and frequency of fallow periods.

Chapter 5

Synthesis

5.1 Contribution of the study to the body of research on agricultural peats

The results summary for the three conducted experiments is presented in Table 5.1. Across all experiments water table increases led to yield decline, higher DOC production and reduction in peat CO_2 emissions, however, the effects of warming on yield and DOC concentrations were mixed. There was no clear pattern in CH_4 emissions when comparing the outcomes of the same treatment, pointing to the underlying difficulty in upscaling CH_4 fluxes from agricultural peats.

Variable	Experiment	Rh	CH_4	DOC pore water	DOC drainage	Yield
Water table	Radish 50→30	↓	↑	-	-	↓
	Celery 50→30	↓	≈	-	↑	↓
	Romaine lettuce 50→30	↓	ox↓	↑	↑	↓
	Romaine lettuce 50→40	↓	ox↓	↑	↑	↓
Temperature	Celery A→E	↑	≈	-	↑	≈
	Romaine lettuce A→E	↑	ox↓	≈	≈	↑
CO_2 level	Radish aCO_2→eCO_2	-	-	-	-	↓

Table 5.1: Effects of environmental manipulations on GHG emissions, DOC production and crop yield. Rh – soil respiration; yield – weight of fresh biomass of harvestable parts; ↑ or ↓ – increase or decrease; ≈ – no change; ox ↓ – decrease in CH_4 oxidation (uptake); - – not recorded or not important; A, a – ambient; E, e – elevated; 50, 40, 30 – water table levels of -50 cm, -40 cm and -30 cm; 50→30, A→E etc. – comparisons between the base value (-50 cm water table, ambient conditions etc.) and the manipulated value (-30 cm water table, elevated conditions etc.); → – direction of manipulation.

In here I present brief conclusions to the following major questions which were asked in the introduction:

1. Can the same yields be obtained at a higher water table level?

Increasing the water table lowered fresh yield in all three studied crops, although the extent of the decrease varied. The yield decrease in the higher water table treatment (-30 cm) as compared to the field level (-50 cm) was 59% in radish bulbs and 64% in radish leaves. The aboveground biomass of romaine lettuce decreased by 21% (-40 cm) and by 32% (-30 cm) when compared to the field water table. The aboveground biomass of celery was affected to a lesser extent: it was 19% lower in the -30 cm treatment when compared to the field water table level, possibly due to celery being better adapted to waterlogging as a marshland plant (Seale, 1975). The lower harvestable yield of the three studied crops could be related to restricted root penetration, among other factors, which limited nutrient absorption from peat.

2. Will increasing the water table reduce peat C loss as CO_2, CH_4 and DOC?

Increasing the water table decreased Rh in the three experiments, however, there was great variability in the recorded CH_4 emissions. This is exemplified by the percentage of positive fluxes in all CH_4 readings: in radish – 40%, in celery – 21%, in romaine lettuce – 11%. The water table position had a statistically significant effect on the CH_4 flux in the radish and the romaine lettuce experiments, however, there was no relationship between the water table and CH_4 emissions in the celery experiment. This makes it difficult to reach a conclusion about the impact of the applied treatments on emissions of CH_4, and, consequently, estimate the total C loss from the system. Raising the water table from the field level to -30 cm or -40 cm increased the concentration of DOC in topsoil pore water by one-third, however, it remains uncertain how much of the pore water DOC is lost from the system by seeping into groundwater and being washed out into the drainage works.

3. <u>How will climate change affect crop yield in the Fens?</u>

The three experiments showed that the extent to which the global warming will affect harvestable yield will very much depend on the crop, the season when it is planted and the magnitude of temperature increase. A moderate warming of 2°C can increase yields (as shown in the romaine lettuce experiment), however, an extreme warming of 5°C may not result in improved yields (as shown in the celery experiment), possibly due to higher transpiration from the crop. The elevated atmospheric CO_2 concentration depressed the yield of radish, which is was an unexpected finding and one that warrants more investigation in future studies.

4. <u>How will climate change affect peat loss and C cycling?</u>

Warming associated with the climate change increased C loss as CO_2 in the three experiments: consequently, the lifespan of agricultural fields of the Fens will be shortened. A moderate warming of 2°C had no effect on DOC production in topsoil pore water, however, an extreme warming value of 5°C increased DOC concentration in drainge water by 45%. Once again, the variability in the CH_4 flux values makes it difficult to generalise about the future CH_4 emissions from agricultural peats. However, the warming of 2°C and 5°C seemed to favour proliferation of methanogens over methanotrophs: the CH_4 consumption rate was one-third lower in the +2°C treatment as compared to the ambient conditions (Chapter 4) and CH_4 emissions more than doubled in the +5°C treatment when compared to the ambient (Chapter 3).

5.3 Research limitations

The experimental set-ups presented in this body of work do not fully represent the field conditions, therefore the values which I obtained may be under- or over-estimated. First of all, the even distribution of temperature in the peat cores is unlike the field conditions (where the temperature falls with depth during the growth season) and likely led to the overestimation of peat oxidation and DOC production. Another consequence of the constant temperature along the peat profile could have been lower values of soil water content as a result of higher rates of evaporative loss from peat. The even temperature distribution within the peat cores could have contributed to intensified root production along the whole soil profile (Weltzin et al., 2000; Zhou et al., 2012), which would increase root respiration. The air temperature in the radish (Chapter 2) and the celery (Chapter 3) experiments was uniform between the day and the night cycles, which could have contributed to overestimation of GHG emissions, as night temperature readings are lower in the field. For the sake of uniformity in PAR between the two growth chambers, the light quality in the three experiments did not precisely correspond to the field conditions, where periods of intense radiation are intermitted by shading by clouds and from neighbouring plants. Shading may change the onset and duration of plant development stages and alter leaf and stem elongation (Fournier and Andrieu, 2000; Ballar and Pierik, 2017). A typical plant shade-avoidance response is for leaves and stems to become more erect (Smith and Whitelam, 1997; Kim et al., 2005; Casal, 2012). The absence of this effect was evident in the celery and the romaine lettuce plants, which were horizontally spread out. As a consequence, the whole-plant photosynthesis could have been potentially affected as the angle of PAR reception was different from the field conditions.

5.4 Policy recommendations and future research

It was not possible to reconcile raising the water table depth (from -50 cm to -30 cm and -40 cm) with the same quantity of yield as obtained at the field level in the three experiments presented in this body of work, however, there may be more options of preserving the agricultural peats of the Fens. More research needs to be done regarding their viability. Increasing the water table would require less water to be pumped out, which would reduce the costs of electricity usage. A cost analysis would need to be performed to assess whether the lower expenditure of maintaining a higher water table outweighs diminished yields of particular crops. Increasing the water table during fallow periods could reduce peat oxidation and consolidation, however, it may lead to accumulation of toxic compounds in soil and nutrient leaching, as described in Chapter 2. More research into peat chemistry following flooding is needed. The finding that the eCO_2 conditions negatively affected the yield of radish (Chapter 2) needs further verification, in particular in the areas of root architecture, root nutrient uptake and soil chemistry in a post-flooding environment.

Given that this body of work revealed the existence of a trade-off between peat preservation and crop yield, farmers of the Fens should decide how much value they place on the longevity of their fields versus short-term economic gain. If long-term agricultural use of the site is the priority for the farmer, increasing the water table by 10 cm is recommended as it would reduce the rate of peat loss, although at the expense of crop yield, as demonstrated in Chapter 4. Alternatively, another option could be explored, namely increasing the water table off-season, as suggested in Chapter 2. This would limit emissions of CO_2, however, proper drainage during the growth season needs to be ensured, otherwise the crop may perform poorly for reasons outlined in Chapter 2.

Bibliography

Accuweather.com, 2019. Last retrieved on 30.07.2019 from https://www.accuweather.com/en/gb/wisbech/pe13-2/month/321848?monyr=2/01/2019

Adamson, J.K., Scott, W.A. and Rowland, A.P., 1998. The dynamics of dissolved nitrogen in a blanket peat dominated catchment. *Environmental Pollution*, 99, 69-77.

Adaptation Sub-Committee, 2016. UK Climate Change Risk Assessment 2017: synthesis report: priorities for the next five years. Committee on Climate Change. Last retrieved on 30.07.2019 from https://www.theccc.org.uk/tackling-climate-change/preparing-for-climate-change/uk-climate-change-risk-assessment-2017

Aerts, R., and Ludwig, F., 1997. Water-table changes and nutritional status affect trace gas emissions from laboratory columns of peatland soils. *Soil Biology and Biochemistry*, 29, 1691-1698.

Ainsworth, E.A. and Rogers, A., 2007. The response of photosynthesis and stomatal conductance to rising [CO_2]: mechanisms and environmental interactions. *Plant, Cell & Environment*, 30, 258-270.

Alaoui-Sossé, B., Gérard, B., Binet, P., Toussaint, M.L. and Badot, P.M., 2005. Influence of flooding on growth, nitrogen availability in soil, and nitrate reduction of young oak seedlings (*Quercus robur* L.). *Annals of Forest Science*, 62, 593-600.

Alberton, O., Kuyper, T.W. and Gorissen, A., 2005. Taking mycocentrism seriously: mycorrhizal fungal and plant responses to elevated CO_2. *New Phytologist*, 167, 859-868.

Allen, S.E., 1989. Chemical analysis of ecological materials 2nd ed., completely rev., London: Blackwell Scientific.

Allison, S.D., 2005. Cheaters, diffusion and nutrients constrain decomposition by microbial enzymes in spatially structured environments. *Ecology Letters*, 8, 626-635.

Amha, Y. and Bohne, H., 2011. Denitrification from the horticultural peats: effects of pH, nitrogen, carbon, and moisture contents. *Biology and Fertility of Soils*, 47, 293-302.

Amthor, J.S., 1991. Respiration in a future, higher- CO_2 world. *Plant, Cell & Environment*, 14, 13-20.

Andert, J., Borjesson, G. and Hallin, S., 2012. Temporal changes in methane oxidizing and denitrifying communities and their activities in a drained peat soil. *Wetlands*, 32, 1047-1055.

Aranjuelo, I., Pérez, P., Hernández, L., Irigoyen, J.J., Zita, G., Martínez-Carrasco, R. and Sánchez-Díaz, M., 2005. The response of nodulated alfalfa to water supply, temperature and elevated CO_2: photosynthetic downregulation. *Physiologia Plantarum*, 123, 348-358.

Armstrong, A., Holden, J., Luxton, K., and Quinton, J.N., 2012. Multi-scale relationship between peatland vegetation type and dissolved organic carbon concentration. *Ecological Engineering*, 47, 182-188.

Arndal, M.F., Tolver, A., Larsen, K.S., Beier, C., and Schmidt, I.K., 2018. Fine Root Growth and Vertical Distribution in Response to Elevated CO_2, Warming and Drought in a Mixed Heathland–Grassland. *Ecosystems*, 21, 15–30.

Adaptation Sub-Committee, 2016. UK Climate Change Risk Assessment 2017: synthesis report: priorities for the next five years. Committee on Climate Change. Last retrieved on 30.07.2019 from https://www.theccc.org.uk/tackling-climate-change/preparing-for-climate-change/uk-climate-change-risk-assessment-2017

Asif, M., Tunc, C.E. and Ozturk, L., 2018. Changes in yield attributes and K allocation in wheat as affected by K deficiency and elevated CO_2. *Plant and Soil*, 426, 153-162.

Aslan-Sungur, G., Lee, X., Evrendilek, F., and Karakaya, N., 2016. Large interannual variability in net ecosystem carbon dioxide exchange of a disturbed temperate peatland. *Science of the Total Environment*, 554, 192-202.

Aydin, G., Karakurt, I. and Aydiner, K., 2010. Evaluation of geologic storage options of CO_2: Applicability, cost, storage capacity and safety. *Energy Policy*, 38, 5072-5080.

Bader, C., Müller, M., Schulin, R. and Leifeld, J., 2018. Peat decomposability in managed organic soils in relation to land use, organic matter composition and temperature. *Biogeosciences*, 15, 703–719.

Baker, A., Cumberland, S. and Hudson, N., 2008. Dissolved and total organic and inorganic carbon in some British rivers. *Area*, 40 117-127.

Banaś, K., and Gos, K., 2004. Effect of peat-bog reclamation on the physico-chemical characteristics of the ground water in peat. *Polish Journal of Ecology*, 52, 69–74.

Basiliko, N., Stewart, H., Roulet, N.T. and Moore, T.R., 2012. Do root exudates enhance peat decomposition? *Geomicrobiology Journal*, 29, 374-378.

Bates, Maechler and Bolker, 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-6. http://CRAN.R-project.org/package=lme4

Batts, G.R., Ellis, R.H., Morison, J.I.L., Nkemka, P.N., Gregory, P.J. and Hadley, P., 1998. Yield and partitioning in crops of contrasting cultivars of winter wheat in response to CO_2 and temperature in field studies using temperature gradient tunnels. *The Journal of Agricultural Science*, 130, 17-27.

Bengtsson, G., Bengtson, P. and Månsson, K.F., 2003. Gross nitrogen mineralization-, immobilization-, and nitrification rates as a function of soil C/N ratio and microbial activity. *Soil Biology and Biochemistry*, 35, 143-154.

Billett, M.F., Charman, D.J., Clark, J.M., Evans, C.D., Evans, M.G., Ostle, N.J., Worrall, F., Burden, A., Dinsmore, K.J., Jones, T. and McNamara, N.P., 2010. Carbon balance of UK peatlands: current state of knowledge and future research challenges. *Climate Research*, 45, 13-29.

Boomer, K.M.B. and Bedford, B.L., 2008. Influence of nested groundwater systems on reduction–oxidation and alkalinity gradients with implications for plant nutrient availability in four New York fens. *Journal of Hydrology*, 351, 107-125.

Bouwman, A.F., 1998. Environmental science: Nitrogen oxides and tropical agriculture. *Nature*, 392, 866.

Britto, D.T. and Kronzucker, H.J., 2002. NH_4^+ toxicity in higher plants: a critical review. *Journal of Plant Physiology*, 159, 567-584.

Bubier, J., Crill, P., Mosedale, A., Frolking, S., and Linder, E., 2003. Peatland responses to varying interannual moisture conditions as measured by automatic CO_2 chambers. *Global Biogeochemical Cycles*, 17.

Bunce, J.A., 1992. Stomatal conductance, photosynthesis and respiration of temperate deciduous tree seedlings grown outdoors at an elevated concentration of carbon dioxide. *Plant, Cell & Environment*, 15, 541-549.

Burton, R.G.O. and Hodgson, J.M. eds., 1987. Lowland peat in England and Wales. Harpenden, UK: Soil Survey of England and Wales.

Butenhoff, C.L. and Khalil, M.A.K., 2007. Global methane emissions from terrestrial plants. *Environmental Science & Technology*, 41, 4032-4037.

Campbell, J.E. and Fourqurean, J.W., 2018. Does Nutrient Availability Regulate Seagrass Response to Elevated CO_2? *Ecosystems*, 21, 1269-1282.

Carlson, K.M., Gerber, J.S., Mueller, N.D., Herrero, M., MacDonald, G.K., Brauman, K.A., Havlik, P., O'Connell, C.S., Johnson, J.A., Saatchi, S. and West, P.C., 2017. Greenhouse gas emissions intensity of global croplands. *Nature Climate Change*, 7, 63.

Carter, E.K., Melkonian, J., Riha, S.J. and Shaw, S.B., 2016. Separating heat stress from moisture stress: analyzing yield response to high temperature in irrigated maize. *Environmental Research Letters*, 11, 094012.

Chalmers, A.G., Sinclair, A.H. and Carver, M., 1999. Nutrients other than nitrogen, phosphorus and potassium (NPK) for cereals. Home Grown Cereals Authority.

Chapin, F.S., Matson, P.A. and Vitousek, P.M., 2012. Principles of Terrestrial Ecosystem Ecology. Springer, New York.

Chen, S., Liu, Y., Zhai, X. and Hu, Z., 2017. Experimental Warming Effects on Soil Respiration, Nitrification, and Denitrification in a Winter Wheat-Soybean Rotation Cropland. *Communications in Soil Science and Plant Analysis*, 48, 148-161.

Chow, A.T., Tanji, K.K., Gao, S., and Dahlgren, R.A., 2006. Temperature, water content and wet–dry cycle effects on DOC production and carbon mineralization in agricultural peat soils. *Soil Biology and Biochemistry*, 38, 477-488.

Christy, B., Tausz-Posch, S., Tausz, M., Richards, R., Rebetzke, G., Condon, A., McLean, T., Fitzgerald, G., Bourgault, M. and O'Leary, G., 2018. Benefits of increasing transpiration efficiency in wheat under elevated CO_2 for rainfed regions. *Global Change Biology*, 24, 1965-1977.

Clark, J.M., Ashley, D., Wagner, M., Chapman, P.J., Lane, S.N., Evans, C.D. and Heathwaite, A.L., 2009. Increased temperature sensitivity of net DOC production from ombrotrophic peat due to water table drawdown. *Global Change Biology*, 15, 794-807.

Clay, G.D., Dixon, S., Evans, M.G., Rowson, J.G. and Worrall, F., 2012. Carbon dioxide fluxes and DOC concentrations of eroding blanket peat gullies. *Earth Surface Processes and Landforms*, 37, 562-571.

Cohen, I., Rapaport, T., Berger, R.T. and Rachmilevitch, S., 2018. The effects of elevated CO_2 and nitrogen nutrition on root dynamics. *Plant Science*, 272, 294-300.

Cotrufo, F.C., Del Galdo, I. and Piermatteo, D., 2009. Litter decomposition: concepts, methods and future perspectives. (In: Soil Carbon Dynamics: An Integrated Methodology, pp. 76-90. (Eds.

W.L. Kutsch, M. Bahn and A. Heinemeyer) Cambridge University Press, Cambridge.

Couwenberg, J., 2009. Methane emissions from peat soil: Facts, MRV-ability, emission factors. Wetlands International, Wageningen.

Crow, S.E., and Wieder, R.K., 2005. Sources of CO_2 emission from a northern peatland: root respiration, exudation, and decomposition. *Ecology*, 86, 1825-1834.

Cui, M., Ma, A., Qi, H., Zhuang, X., Zhuang, G. and Zhao, G., 2015. Warmer temperature accelerates methane emissions from the Zoige wetland on the Tibetan Plateau without changing methanogenic community composition. *Scientific Reports*, 5, 11616.

Cumming, A.M.J., 2018. Multi-annual carbon flux at an intensively cultivated lowland peatland in East Anglia, UK (Doctoral dissertation, Department of Geography). Last retrieved on 30.07.2019 from https://lra.le.ac.uk/handle/2381/43148

Curry, C.L., 2009. The consumption of atmospheric methane by soil in a simulated future climate. *Biogeosciences*, 6, 2355-2367.

Curtis, P.S., 1996. A meta-analysis of leaf gas exchange and nitrogen in trees grown under elevated carbon dioxide. *Plant, Cell & Environment*, 19, 127-137.

Daccache, A., Weatherhead, E.K., Stalham, M.A. and Knox, J.W., 2011. Impacts of climate change on irrigated potato production in a humid climate. *Agricultural and Forest Meteorology*, 151, 1641-1653.

Damman, A.W.H., 1978. Distribution and movement of elements in ombrotrophic peat bogs. *Oikos*, 480-495.

Darby, H. C., 1956. The draining of the Fens. Cambridge University Press.

Das, S. and Adhya, T.K., 2012. Dynamics of methanogenesis and methanotrophy in tropical paddy soils as influenced by elevated CO_2 and temperature interaction. *Soil Biology and Biochemistry*, 47, 36-45.

Dawson, J.J., Tetzlaff, D., Speed, M., Hrachowitz, M. and Soulsby, C., 2011. Seasonal controls on DOC dynamics in nested upland catchments in NE Scotland. *Hydrological Processes*, 25, 1647-1658.

Dawson, Q., Kechavarzi, C., Leeds-Harrison, P.B., Burton, R.G.O., 2010. Subsidence and degradation of agricultural peatlands in the Fenlands of Norfolk, UK. *Geoderma*, 154, 181–187.

Daymond, A.J., Wheeler, T.R., Hadley, P., Ellis, R.H. and Morison, J.I.L., 1997. The growth, development and yield of onion (*Allium cepa* L.) in response to temperature and CO_2. *Journal of Horticultural Science*, 72, 135-145.

Dedysh, S.N., Panikov, N.S., Liesack, W., Großkopf, R., Zhou, J. and Tiedje, J.M., 1998. Isolation of Acidophilic Methane-Oxidizing Bacteria from Northern Peat Wetlands. *Science*, 282, 281-284.

Defra, 2014. United Kingdom areas, production, valuations and trade statistics for fruit and vegetables to 2013 with historic statistics for ornamental plants and flowers. Last retrieved on 30.07.2019 from https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/341921/hort-report-07aug14.pdf

Defra, 2016. Horticulture Statistics 2015. Last retrieved on 30.07.2019 from https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/540165/hort-report-22jul16a.pdf

Defra, 2019. Agriculture in the United Kingdom 2018. Last retrieved on 30.07.2019 from https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/815303/AUK_2018_09jul19.pdf

De Ruijter, F.J., Boumans, L.J.M., Smit, A.L. and Van den Berg, M., 2007. Nitrate in upper groundwater on farms under tillage as affected by fertilizer use, soil type and groundwater table. *Nutrient Cycling in Agroecosystems*, 77, 155-167.

Dimitrov, D.D., Grant, R.F., Lafleur, P.M., and Humphreys, E.R., 2010. Modeling the effects of hydrology on ecosystem respiration at Mer Bleue bog. *Journal of Geophysical Research: Biogeosciences*, 115.

D'imperio, L., Nielsen, C.S., Westergaard-Nielsen, A., Michelsen, A. and Elberling, B., 2017. Methane oxidation in contrasting soil types: responses to experimental warming with implication for landscape-integrated CH_4 budget. *Global Change Biology*, 23, 966-976.

Dinsmore, K.J., Skiba, U.M., Billett, M.F. and Rees, R.M., 2009. Effect of water table on greenhouse gas emissions from peatland mesocosms. *Plant and Soil*, 318, 229-242.

Dirks, B.O.M., Hensen, A., and Goudriaan, J., 2000. Effect of drainage on CO_2 exchange patterns in an intensively managed peat pasture. *Climate Research*, 14, 57-63.

Dixon, S.D., Qassim, S.M., Rowson, J.G., Worrall, F., Evans, M.G., Boothroyd, I.M. and Bonn, A., 2014. Restoration effects on water table depths and CO_2 fluxes from climatically marginal blanket bog. *Biogeochemistry*, 118, 159–176.

Dodds, G.T., Trenholm, L., Rajabipour, A., Madramootoo, C.A. and Norris, E.R., 1997. Yield and quality of tomato fruit under water-table management. *Journal of the American Society for Horticultural Science*, 122, 491-498.

Dowrick, D.J., Freeman, C., Lock, M.A. and Reynolds, B., 2006. Sulphate reduction and the suppression of peatland methane emissions following summer drought. *Geoderma*, 132, 384-390.

Drew, M.C. and Lynch, J., 1980. Soil anaerobiosis, microorganisms, and root function. *Annual Review of Phytopathology*, 18, 37-66.

Drew, M.C. and Sisworo, E.J., 1977. Early effects of flooding on nitrogen deficiency and leaf chlorosis in barley. *New Phytologist*, 79, 567-571.

Du, C., Wang, X., Zhang, M., Jing, J. and Gao, Y., 2019. Effects of elevated CO_2 on plant CNP stoichiometry in terrestrial ecosystems: A meta-analysis. *Science of The Total Environment*, 650, 697-708.

Dufault, R.J., Ward, B. and Hassell, R.L., 2009. Dynamic relationships between field temperatures and romaine lettuce yield and head quality. *Scientia Horticulturae*, 120, 452-459.

Dunfield, P., Dumont, R. and Moore, T.R., 1993. Methane production and consumption in temperate and subarctic peat soils: response to temperature and pH. *Soil Biology and Biochemistry*, 25, 321-326.

Duval, T.P. and Radu, D.D., 2018. Effect of temperature and soil organic matter quality on greenhouse-gas production from temperate poor and rich fen soils. *Ecological Engineering*, 114, 66-75.

El-Jaoual, T. and Cox, D.A., 1998. Manganese toxicity in plants. *Journal of Plant Nutrition*, 21, 353-386.

Else, M. and Atkinson, C., 2010. Climate change impacts on UK top and soft fruit production. *Outlook on Agriculture*, 39, 257-262.

Erbs, M., Manderscheid, R., Jansen, G., Seddig, S., Pacholski, A. and Weigel, H.J., 2010. Effects of free-air CO_2 enrichment and nitrogen supply on grain quality parameters and elemental composition of wheat and barley grown in a crop rotation. *Agriculture, Ecosystems & Environment*, 136, 59-68.

Esteban, R., Ariz, I., Cruz, C. and Moran, J.F., 2016. Mechanisms of ammonium toxicity and the quest for tolerance. *Plant Science*, 248, 92-101.

Estop-Aragonés, C., Knorr, K.H. and Blodau, C., 2012. Controls on in situ oxygen and dissolved inorganic carbon dynamics in peats of a temperate fen. *Journal of Geophysical Research: Biogeosciences*, 117.

Evans, C., Morrison, R., Burden, A., Williamson, J., Baird, A., Brown, E., Callaghan, N., Chapman, P., Cumming, A., Dean, H., Dixon, S., Dooling, G., Evans, J., Gauci, V., Grayson, R., Haddaway, N., He, Y., Heppell, K., Holden, J., Hughes, S., Kaduk, J., Jones, D., Matthews, R., Menichino, N., Misselbrook, T., Page, S., Pan, G., Peacock, M., Rayment, M., Ridley, L., Robinson, I., Rylett, D., Scowen, M., Stanley, K., and Worrall, F., 2016. Final report on project SP1210: Lowland peatland systems in England and Wales – evaluating greenhouse gas fluxes and carbon balances. Centre for Ecology and Hydrology. Last retrieved on 30.07.2019 from http://oro.open.ac.uk/50635

Evans, C.D., Jones, T.G., Burden, A., Ostle, N., Zieliński, P., Cooper, M.D., Peacock, M., Clark, J.M., Oulehle, F., Cooper, D. and Freeman, C., 2012. Acidity controls on dissolved organic carbon mobility in organic soils. *Global Change Biology*, 18, 3317-3331.

Evans, J.R., 1989. Photosynthesis and nitrogen relationships in leaves of C_3 plants. *Oecologia*, 78, 9-19.

Fan, X.X., Xu, Z.G., Liu, X.Y., Tang, C.M., Wang, L.W. and Han, X.L., 2013. Effects of light intensity on the growth and leaf development of young tomato plants grown under a combination of red and blue light. *Scientia Horticulturae*, 153, 50-55.

Fangmeier, A., De Temmerman, L., Black, C., Persson, K. and Vorne, V., 2002. Effects of elevated CO_2 and/or ozone on nutrient concentrations and nutrient uptake of potatoes. *European Journal of Agronomy*, 17, 353-368.

Fangmeier, A., Grüters, U., Högy, P., Vermehren, B. and Jäger, H.J., 1997. Effects of elevated CO_2, nitrogen supply and tropospheric ozone on spring wheat—II. Nutrients (N, P, K, S, Ca, Mg, Fe, Mn, Zn). *Environmental Pollution*, 96, 43-59.

Fenner, N., Freeman, C., Lock, M.A., Harmens, H., Reynolds, B. and Sparks, T., 2007. Interactions between elevated CO_2 and warming could amplify DOC exports from peatland catchments. *Environmental Science & Technology*, 41, 3146-3152.

Fernández, M.D., Tezara, W., Rengifo, E. and Herrera, A., 2002. Lack of downregulation of photosynthesis in a tropical root crop, cassava, grown under an elevated CO_2 concentration. *Functional Plant Biology*, 29, 805-814.

Ferreira, C.J.B., Zotarelli, L., Tormena, C.A., Rens, L.R. and Rowland, D.L., 2017. Effects of water table management on least limiting water range and potato root growth. *Agricultural Water Management*, 186, 1-11.

Ferreira, R.D.C., Bezerra, R.D.S. and Rosa, J.Q., 2014. Effects of light intensity modification by reflective aluminized screenhouse on sweet pepper growth and yield. *Engenharia Agrícola*, 34, 626-635.

Fillery, I.R.P. and Vlek, P.L.G., 1982. The significance of denitrification of applied nitrogen in fallow and cropped rice soils under different flooding regimes I. Greenhouse experiments. *Plant and Soil*, 65, 153-169.

Florio, E.L., Mercau, J.L., Jobbágy, E.G. and Nosetto, M.D., 2014. Interactive effects of water-table depth, rainfall variation, and sowing date on maize production in the Western Pampas. *Agricultural Water Management*, 146, 75–83.

Foy, C.D., Chaney, R.T. and White, M.C., 1978. The physiology of metal toxicity in plants. *Annual Review of Plant Physiology*, 29, 511-566.

Frank, S., Tiemeyer, B., Bechtold, M., Lücke, A. and Bol, R., 2017. Effect of past peat cultivation practices on present dynamics of dissolved organic carbon. *Science of the Total Environment*, 574, 1243-1253.

Frank, S., Tiemeyer, B., Gelbrecht, J., and Freibauer, A., 2014. High soil solution carbon and nitrogen concentrations in a drained Atlantic bog are reduced to natural levels by 10 years of rewetting. *Biogeosciences*, 11, 2309.

Frantz, J.M., Ritchie, G., Cometti, N.N., Robinson, J. and Bugbee, B., 2004. Exploring the limits of crop productivity: beyond the limits of tipburn in lettuce. *Journal of the American Society for Horticultural Science*, 129, 331-338.

Freeman, C., Evans, C.D., Monteith, D.T., Reynolds, B. and Fenner, N., 2001. Export of organic carbon from peat soils. *Nature*, 412, 785.

Frolking, S., Roulet, N.T., Moore, T.R., Lafleur, P.M., Bubier, J.L., and Crill, P.M., 2002. Modeling seasonal to annual carbon balance of Mer Bleue Bog, Ontario, Canada. *Global Biogeochemical Cycles*, 16, 4-1.

Gibson, H.S., Worrall, F., Burt, T.P. and Adamson, J.K., 2009. DOC budgets of drained peat catchments: implications for DOC production in peat soils. *Hydrological Processes: An International Journal*, 23, 1901-1911.

Gifford, R.M., 1977. Growth pattern, carbon dioxide exchange and dry weight distribution in wheat growing under differing photosynthetic environments. *Functional Plant Biology*, 4, 99-110.

Gifford, R.M., Barrett, D.J. and Lutze, J.L., 2000. The effects of elevated [CO_2] on the C:N and C:P mass ratios of plant tissues. *Plant and Soil*, 224, 1-14.

Gigon, A. and Rorison, I.H., 1972. The response of some ecologically distinct plant species to nitrate-and to ammonium-nitrogen. *The Journal of Ecology*, 93-102.

Gill, A.L., Giasson, M.A., Yu, R. and Finzi, A.C., 2017. Deep peat warming increases surface methane and carbon dioxide emissions in a black spruce-dominated ombrotrophic bog. *Global Change Biology*, 23, 5398-5411.

Girkin, N.T., Turner, B.L., Ostle, N., Craigon, J. and Sjögersten, S., 2018. Root exudate analogues accelerate CO_2 and CH_4 production in tropical peat. *Soil Biology and Biochemistry*, 117, 48-55.

Global Environmental Centre, 2008. Assessment on peatlands, biodiversity and climate change. Main report. Global Environmental Centre, Petaling Jaya. Last retrieved on 30.07.2019 from http://www.imcg.net/media/download_gallery/books/assessment_peatland.pdf

Gnatowski, T., Szatylowicz, J. and Brandyk, T., 2002. Effect of peat decomposition on the capillary rise in peat-moorsh soils from the Biebrza River Valley. *International Agrophysics*, 16, 97-102.

Green, S.M., Baird, A.J., Boardman, C.P., and Gauci, V., 2014. A mesocosm study of the effect of restoration on methane (CH_4) emissions from blanket peat. *Wetlands Ecology and Management*, 22, 523-537.

Gu, C., Zhang, S., Han, P., Hu, X., Xie, L., Li, Y., Brooks, M., Liao, X. and Qin, L., 2019. Soil enzyme activity in soils subjected to flooding and the effect on nitrogen and phosphorus uptake by Oilseed rape. *Frontiers in Plant Science*, 10, 368.

Gundersen, P., Callesen, I. and De Vries, W., 1998. Nitrate leaching in forest ecosystems is related to forest floor CN ratios. *Environmental Pollution*, 102, 403-407.

Hallema, D.W., Lafond, J.A., Périard, Y., Gumiere, S.J., Sun, G. and Caron, J., 2015. Long-term effects of peatland cultivation on soil physical and hydraulic properties: Case study in Canada. *Vadose Zone Journal*, 14.

Harrison, A.F., Taylor, K., Scott, A., Poskitt, J.A.N., Benham, D., Grace, J., Chaplow, J. and Rowland, P., 2008. Potential effects of climate change on DOC release from three different soil types on the Northern Pennines UK: examination using field manipulation experiments. *Global Change Biology*, 14, 687-702.

Hay, R.K.M. and Porter, J.R., 2006. The physiology of crop yield. Blackwell Publishing.

He, J., Tan, L.P. and Lee, S.K., 2009. Root-zone temperature effects on photosynthesis, ^{14}C-photoassimilate partitioning and growth of temperate lettuce (*Lactuca sativa* cv. 'Panama') in the tropics. *Photosynthetica*, 47, 95-103.

Heißner, A., Schmidt, S., Schonhof, I., Feller, C., and Schreiner, M., 2006. Spear yield and quality of white asparagus as affected by soil temperature. *European Journal of Agronomy*, 25, 336-344.

Hemes, K.S., Chamberlain, S.D., Eichelmann, E., Anthony, T., Valach, A., Kasak, K., Szutu, D., Verfaillie, J., Silver, W.L. and Baldocchi, D.D., 2019. Assessing the carbon and climate benefit of restoring degraded agricultural peat soils to managed wetlands. *Agricultural and Forest Meteorology*, 268, 202-214.

Hodge, C.A.H., Burton, R.GO., Corbett, W.M., Evans, R. and Seale, R.S., 1984. Soils and their use in Eastern England, Harpenden: Soil Survey of England and Wales.

Holden, J., Chapman, P.J. and Labadz, J.C., 2004. Artificial drainage of peatlands: hydrological and hydrochemical process and wetland restoration. *Progress in Physical Geography*, 28, 95-123.

Holman, I.P., and Kechavarzi, C., 2011. A revised estimate of peat reserves and loss in the East Anglian Fens Commissioned by the RSPB.

Hou, C., Song, C., Li, Y., Wang, J., Song, Y. and Wang, X., 2013. Effects of water table changes on soil CO_2, CH_4 and N_2O fluxes during the growing season in freshwater marsh of Northeast China. *Environmental Earth Sciences*, 69, 1963–1971.

Houshmandfar, A., Fitzgerald, G.J., Armstrong, R., Macabuhay, A.A. and Tausz, M., 2015. Modelling stomatal conductance of wheat: An assessment of response relationships under elevated CO_2. *Agricultural and Forest Meteorology*, 214, 117-123.

Hu, C., Tian, Z., Gu, S., Guo, H., Fan, Y., Abid, M., Chen, K., Jiang, D., Cao, W. and Dai, T., 2018. Winter and spring night-warming improve root extension and soil nitrogen supply to increase nitrogen uptake and utilization of winter wheat (*Triticum aestivum* L.). *European Journal of Agronomy*, 96, 96-107.

Huang, X., Shabala, S., Shabala, L., Rengel, Z., Wu, X., Zhang, G. and Zhou, M., 2015. Linking waterlogging tolerance with Mn^{2+} toxicity: a case study for barley. *Plant Biology*, 17, 26-33.

Idso, S.B., Kimball, B.A. and Mauney, J.R., 1988. Effects of atmospheric CO_2 enrichment on root: shoot ratios of carrot, radish, cotton and soybean. *Agriculture, Ecosystems & Environment*, 21, 293-299.

Idso, S.B. and Kimball, B.A., 1989. Growth response of carrot and radish to atmospheric CO_2 enrichment. *Environmental and Experimental Botany*, 29, 135-139.

IPCC, 2014b: 2013 Supplement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories: Wetlands, Hiraishi, T., Krug, T., Tanabe, K., Srivastava, N., Baasansuren, J., Fukuda, M. and Troxler, T.G. (eds). Published: IPCC, Switzerland.

IPCC, 2014c: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland.

IPCC, 2014a: Summary for policymakers. In: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Field, C.B., V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, and L.L.White (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 1-32.

IPCC, 2018: Summary for Policymakers. In: Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty [Masson-Delmotte, V., P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J.B.R. Matthews, Y. Chen, X. Zhou, M.I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, and T. Waterfield (eds.)]. In Press.

Itoh, H., Hayashi, S., Nakajima, T., Hayashi, T., Yoshida, H., Yamazaki, K. and Komatsu, T., 2009. Effects of soil type, vertical root distribution and precipitation on grain yield of winter wheat. *Plant Production Science*, 12, 503-513.

Iversen, C.M., Childs, J., Norby, R.J., Ontl, T.A., Kolka, R.K., Brice, D.J., McFarlane, K.J. and Hanson, P.J., 2018. Fine-root growth in a forested bog is seasonally dynamic, but shallowly distributed in nutrient-poor peat. *Plant and Soil*, 424, 123-143.

Järveoja, J., Peichl, M., Maddison, M., Soosaar, K., Vellak, K., Karofeld, E. and Mander, Ü., 2016. Impact of water table level on annual carbon and greenhouse gas balances of a restored peat extraction area. *Biogeosciences*, 13, 2637-2651.

Jenkins, G.J., Perry, M.C., and Prior, M.J., 2008. The climate of the United Kingdom and recent trends. Met Office Hadley Centre, Exeter, UK. Last retrieved on 30.07.2019 from https://ukcip.ouce.ox.ac.uk/wp-content/PDFs/UKCP09_Trends.pdf

Jia, X., Liu, T., Zhao, Y., He, Y. and Yang, M., 2016. Elevated atmospheric CO_2 affected photosynthetic products in wheat seedlings and biological activity in rhizosphere soil under cadmium stress. *Environmental Science and Pollution Research*, 23, 514-526.

Jia, X., Wang, W., Chen, Z., He, Y. and Liu, J., 2014. Concentrations of secondary metabolites in tissues and root exudates of wheat seedlings changed under elevated atmospheric CO_2 and cadmium-contaminated soils. *Environmental and Experimental Botany*, 107, 134-143.

Jungkunst, H.F., Flessa, H., Scherber, C. and Fiedler, S., 2008. Groundwater level controls CO_2, N_2O and CH_4 fluxes of three different hydromorphic soil types of a temperate forest ecosystem. *Soil Biology and Biochemistry*, 40, 2047-2054.

Juszczak, R., Humphreys, E., Acosta, M., Michalak-Galczewska, M., Kayzer, D. and Olejnik, J., 2013. Ecosystem respiration in a heterogeneous temperate peatland and its sensitivity to peat temperature and water table depth. *Plant and Soil*, 366, 505-520.

Kandel, T.P., Lærke, P.E. and Elsgaard, L., 2018. Annual emissions of CO_2, CH_4 and N_2O from a temperate peat bog: Comparison of an undrained and four drained sites under permanent grass and arable crop rotations with cereals and potato. *Agricultural and Forest Meteorology*, 256, 470-481.

Karki, S., Elsgaard, L., Kandel, T. P. and Lærke, P. E., 2016. Carbon balance of rewetted and drained peat soils used for biomass production: a mesocosm study. *GCB Bioenergy*, 8, 969–980.

Kechavarzi, C., Dawson, Q., Leeds-Harrison, P.B., Szatyłowicz, J. and Gnatowski, T., 2007. Water table management in lowland UK peat soils and its potential impact on CO_2 emission. *Soil Use and Management*, 23, 359-367.

Kim, S.Y., Freeman, C., Fenner, N. and Kang, H., 2012. Functional and structural responses of bacterial and methanogen communities to 3-year warming incubation in different depths of peat mire. *Applied Soil Ecology*, 57, 23-30.

Kirk, G.J.D., 2004. Biogeochemistry of Submerged Soils, Wiley.

Klemedtsson, L., Von Arnold, K., Weslien, P. and Gundersen, P., 2005. Soil CN ratio as a scalar parameter to predict nitrous oxide emissions. *Global Change Biology*, 11, 1142-1147.

Knorr, K.H., Lischeid, G. and Blodau, C., 2009. Dynamics of redox processes in a minerotrophic fen exposed to a water table manipulation. *Geoderma*, 153, 379-392.

Knox, J., Morris, J. and Hess, T., 2010. Identifying future risks to UK agricultural crop production: Putting climate change in context. *Outlook on Agriculture*, 39, 249-256.

Knox, S.H., Sturtevant, C., Matthes, J.H., Koteen, L., Verfaillie, J. and Baldocchi, D., 2015. Agricultural peatland restoration: effects of land-use change on greenhouse gas (CO_2 and CH_4) fluxes in the Sacramento-San Joaquin Delta. *Global Change Biology*, 21, 750-765.

Koelbener, A., Ström, L., Edwards, P.J. and Venterink, H.O., 2010. Plant species from mesotrophic wetlands cause relatively high methane emissions from peat soil. *Plant and Soil*, 326, 147-158.

Koops, J.G., Oenema, O. and Van Beusichem, M.L., 1996. Denitrification in the top and sub soil of grassland on peat soils. *Plant and Soil*, 184, 1-10.

Kriedemann, P.E., Sward, R.J. and Downton, W.J.S., 1976. Vine response to carbon dioxide enrichment during heat therapy. *Functional Plant Biology*, 3, 605-618.

Kubiske, M.E. and Pregitzer, K.S., 1996. Effects of elevated CO_2 and light availability on the photosynthetic light response of trees of contrasting shade tolerance. *Tree Physiology*, 16, 351-358.

Kumar, A., Nayak, A.K., Das, B.S., Panigrahi, N., Dasgupta, P., Mohanty, S., Kumar, U., Panneerselvam, P. and Pathak, H., 2019. Effects of water deficit stress on agronomic and physiological responses of rice and greenhouse gas emission from rice soil under elevated atmospheric CO_2. *Science of the Total Environment*. 650, 2032-2050.

Kutsch, W.L., Schmiel, J. and Denef, K., 2009. Measuring soil microbial parameters relevant for soil carbon fluxes. (In: Soil Carbon Dynamics: An Integrated Methodology, pp. 169-186. (Eds. W.L. Kutsch, M. Bahn and A. Heinemeyer) Cambridge University Press, Cambridge.

Laanbroek, H.J., 2009. Methane emission from natural wetlands: interplay between emergent macrophytes and soil microbial processes. A mini-review. *Annals of Botany*, 105, 141-153.

Lafleur, P.M., Moore, T.R., Roulet, N.T. and Frolking, S., 2005. Ecosystem respiration in a cool temperate bog depends on peat temperature but not water table. *Ecosystems*, 8, 619-629.

Le Mer, J. and Roger, P., 2001. Production, oxidation, emission and consumption of methane by soils: A review. *European Journal of Soil Biology*, 37, 25-50.

Leroy, F., Gogo, S., Guimbaud, C., Bernard-Jannin, L., Hu, Z., and Laggoun-Défarge, F., 2017. Vegetation composition controls temperature sensitivity of CO_2 and CH_4 emissions and DOC concentration in peatlands. *Soil Biology and Biochemistry*, 107, 164-167.

Li, F., Xie, Y., Yang, G., Zhu, L., Hu, C., Chen, X. and Deng, Z., 2017. Interactive influence of water level, sediment heterogeneity, and plant density on the growth performance and root characteristics of *Carex brevicuspis*. *Limnologica*, 62, 111-117.

Li, Z., Tang, S., Deng, X., Wang, R. and Song, Z., 2010. Contrasting effects of elevated CO_2 on Cu and Cd uptake by different rice varieties grown on contaminated soils with two levels of metals: implication for phytoextraction and food safety. *Journal of Hazardous Materials*, 177, 352-361.

Liimatainen, M., Voigt, C., Martikainen, P.J., Hytönen, J., Regina, K., Óskarsson, H. and Maljanen, M., 2018. Factors controlling nitrous oxide emissions from managed northern peat soils with low carbon to nitrogen ratio. *Soil Biology and Biochemistry*, 122, 186-195.

Liu, B.B., Li, M., Li, Q.M., Cui, Q.Q., Zhang, W.D., Ai, X.Z. and Bi, H.G., 2018. Combined effects of elevated CO_2 concentration and drought stress on photosynthetic performance and leaf structure of cucumber (*Cucumis sativus* L.) seedlings. *Photosynthetica*, 56, 942-952.

Liu, H. and Lennartz, B., 2019. Hydraulic properties of peat soils along a bulk density gradient—A meta study. *Hydrological Processes*, 33, 101-114.

Liu, L., Chen, H., Zhu, Q., Yang, G., Zhu, E., Hu, J., Peng, C., Jiang, L., Zhan, W., Ma, T. and He, Y., 2016. Responses of peat carbon at different depths to simulated warming and oxidizing. *Science of the Total Environment*, 548, 429-440.

Loeb, R., Lamers, L.P. and Roelofs, J.G., 2008. Effects of winter versus summer flooding and subsequent desiccation on soil chemistry in a riverine hay meadow. *Geoderma*, 145, 84-90.

Lorenz, H.P. and Wiebe, H.J., 1980. Effect of temperature on photosynthesis of lettuce adapted to different light and temperature conditions. *Scientia Horticulturae*, 13, 115-123.

Lumsdon, D.G., Stutter, M.I., Cooper, R.J. and Manson, J.R., 2005. Model assessment of biogeochemical controls on dissolved organic carbon partitioning in an acid organic soil. *Environmental Science & Technology*, 39, 8057-8063.

Lundin, L., Nilsson, T., Jordan, S., Lode, E. and Strömgren, M., 2017. Impacts of rewetting on peat, hydrology and water chemical composition over 15 years in two finished peat extraction areas in Sweden. *Wetlands Ecology and Management*, 25, 405-419.

Luo, Y. and Zhou, X., 2006. Soil Respiration and the Environment. Academic Press, London.

Lynch, J.M., 1978. Production and phytotoxicity of acetic acid in anaerobic soils containing plant residues. *Soil Biology and Biochemistry*, 10, 131-135.

Ma, H., Zou, D., Wen, J., Ji, Z., Gong, J. and Liu, C., 2018b. The impact of elevated atmospheric CO_2 on cadmium toxicity in *Pyropia haitanensis* (Rhodophyta). *Environmental Science and Pollution Research*, 25, 33361-33369.

Ma, X.X., Yan, Y., Hong, J.T., Lu, X.Y. and Wang, X.D., 2017. Impacts of warming on root biomass allocation in alpine steppe on the north Tibetan Plateau. *Journal of Mountain Science*, 14, 1615-1623.

Ma, Z., Flynn, J., Libra, G. and Zechuan, S.H.I., 2018a. Elevated CO_2 accelerates phosphorus depletion by common bean (*Phaseolus vulgaris*) in association with altered leaf biochemical properties. *Pedosphere*, 28, 422-429.

Mackereth, F.J.H., Heron, J. and Talling, J.F., 1989. Water Analysis: Some Revised Methods for Limnologists (Second Impression).

Maljanen, M., Hytönen, J., Mäkiranta, P., Alm, J., Minkkinen, K., Laine, J., and Martikainen, P.J., 2007. Greenhouse gas emissions from cultivated and abandoned organic croplands in Finland. *Boreal Environment Research*, 12, 133-140.

Maljanen, M., Komulainen, V.M., Hytönen, J., Martikainen, P.J. and Laine, J., 2004. Carbon dioxide, nitrous oxide and methane dynamics in boreal organic agricultural soils with different soil characteristics. *Soil Biology and Biochemistry*, 36, 1801-1808.

Maljanen, M., Sigurdsson, B.D., Guðmundsson, J., Óskarsson, H., Huttunen, J.T. and Martikainen, P.J., 2010. Greenhouse gas balances of managed peatlands in the Nordic countries - present knowledge and gaps. *Biogeosciences*, 7, 2711-2738.

Mansfeldt, T., 2003. In situ long-term redox potential measurements in a dyked marsh soil. *Journal of Plant Nutrition and Soil Science*, 166, 210-219.

Marchin, R.M., Broadhead, A.A., Bostic, L.E., Dunn, R.R., and Hoffmann, W.A., 2016. Stomatal acclimation to vapour pressure deficit doubles transpiration of small tree seedlings with warming. *Plant, Cell & Environment*, 39, 2221-2234.

Marschner, H., 2011. Marschner's mineral nutrition of higher plants. Academic Press.

Marty, C., Houle, D., Gagnon, C. and Courchesne, F., 2017. The relationships of soil total nitrogen concentrations, pools and C:N ratios with climate, vegetation types and nitrate deposition in temperate and boreal forests of eastern Canada. *Catena*, 152, 163-172.

Matsuo, K., Ae, N. and Vorachit, S., 2017. Reducing the Risk of Iron Toxicity by Imposing Unsaturated Conditions before Flooding. *Communications in Soil Science and Plant Analysis*, 48, 1078-1088.

Matsuo, N., Takahashi, M., Yamada, T., Takahashi, M., Hajika, M., Fukami, K. and Tsuchiya, S., 2017. Effects of water table management and row width on the growth and yield of three soybean cultivars in southwestern Japan. *Agricultural Water Management*, 192, 85-97.

Matysek, M., Leake, J., Banwart, S., Johnson, I., Page, S., Kaduk, J., Smalley, A., Cumming, A. and Zona, D., 2019. Impact of fertiliser, water table, and warming on celery yield and CO_2 and CH_4 emissions from fenland agricultural peat. *Science of The Total Environment*, 667, 179-190.

McDonald, I.R., Hall, G.H., Pickup, R.W. and Murrell, J.C., 1996. Methane oxidation potential and preliminary analysis of methanotrophs in blanket bog peat using molecular ecology techniques. *FEMS Microbiology Ecology*, 21, 197-211.

McEwing, K.R., Fisher, J.P. and Zona, D., 2015. Environmental and vegetation controls on the spatial variability of CH_4 emission from wet-sedge and tussock tundra ecosystems in the Arctic. *Plant and Soil*, 388, 37-52.

McGranahan, D.A. and Poling, B.N., 2018. Trait-based responses of seven annual crops to elevated CO_2 and water limitation. *Renewable Agriculture and Food Systems*, 33, 259-266.

McGrath, J.M. and Lobell, D.B., 2013. Reduction of transpiration and altered nutrient allocation contribute to nutrient decline of crops grown in elevated CO_2 concentrations. *Plant, Cell & Environment,* 36, 697-705.

Miller, J.D., Adamson, J.K. and Hirst, D., 2001. Trends in stream water quality in Environmental Change Network upland catchments: the first 5 years. *Science of the Total Environment*, 265, 27-38.

Minichin, P.E.H., Thorpe, M.R. and Farrar, J.F., 1994. Short-term control of root:shoot partitioning. *Journal of Experimental Botany*, 45, 615-622.

Moore, T.R., Bubier, J.L., Frolking, S.E., Lafleur, P.M., and Roulet, N.T., 2002. Plant biomass and production and CO_2 exchange in an ombrotrophic bog. *Journal of Ecology*, 90, 25-36.

Moore, T.R., and Dalva, M., 2001. Some controls on the release of dissolved organic carbon by plant tissues and soils. *Soil Science*, 166, 38-47.

Moraghan, J.T., 1985. Manganese Deficiency in Soybeans as Affected by FeEddha and Low Soil Temperature 1. *Soil Science Society of America Journal*, 49, 1584-1586.

Moran, M.A. and Zepp, R.G., 1997. Role of photoreactions in the formation of biologically labile compounds from dissolved organic matter. *Limnology and Oceanography*, 42, 1307-1316.

Morling, K., Raeke, J., Kamjunke, N., Reemtsma, T. and Tittel, J., 2017. Tracing aquatic priming effect during microbial decomposition of terrestrial dissolved organic carbon in chemostat experiments. *Microbial Ecology*, 74, 534-549.

Morrison, R., Cumming, A.M.J., Taft, H.E., Kaduk, J., Page S.E., Jones, D.L., Harding, R.J., and Balzter, H., 2013. Carbon dioxide fluxes at an intensively cultivated temperate lowland peatland in the East Anglian Fens, UK, *Biogeosciences Discuss.*, 10, 4193–4223.

Muhr, J., Höhle, J., Otieno, D.O. and Borken, W., 2016. Manipulative lowering of the water table during summer does not affect CO_2 emissions and uptake in a fen in Germany. *Ecological Applications*, 21, 391–401.

Mulvaney, R.L., 1996. Nitrogen – Inorganic forms. p. 1123-1184. In D.L. Sparks et al. (eds.) Methods of soil analysis. Part 2. Chemical properties. SSSA Book Ser. 5. Soil Sci. Soc. Am., Madison, WI.

Munir, T.M., Khadka, B., Xu, B. and Strack, M., 2017. Mineral nitrogen and phosphorus pools affected by water table lowering and warming in a boreal forested peatland. Ecohydrology, 10, 1893.

Murphy, M., Laiho, R. and Moore, T.R., 2009. Effects of water table drawdown on root production and aboveground biomass in a boreal bog. *Ecosystems*, 12, 1268-1282.

Murphy, M.T. and Moore, T.R., 2010. Linking root production to aboveground plant characteristics and water table in a temperate bog. *Plant and Soil*, 336, 219-231.

Musarika, S., Atherton, C.E., Gomersall, T., Wells, M.J., Kaduk, J., Cumming, A.M. J.and Zona, D., 2017. Effect of water table management and elevated CO_2 on radish productivity and on CH_4 and CO_2 fluxes from peatlands converted to agriculture. *Science of The Total Environment*, 584, 665-672.

Natural England, 2010. England's peatlands: carbon storage and greenhouse gases. Natural England Report NE257. Last retrieved on 30.07.2019 from http://publications.naturalengland.org.uk/publication/30021

Natural England, 2015. National Character Area profile: The Fens. Last retrieved on 30.07.2019 from http://publications.naturalengland.org.uk/publication/6229624

NFU, 2019. Why farming matters in the Fens. Last retrieved on 30.07.2019 from http://www.nfuonline.com/assets/23991

Niedermeier, A. and Robinson, J.S., 2007. Hydrological controls on soil redox dynamics in a peat-based, restored wetland. *Geoderma*, 137, 318-326.

Norberg, L., Berglund, Ö. and Berglund, K., 2016. Nitrous oxide and methane fluxes during the growing season from cultivated peat soils, peaty marl and gyttja clay under different cropping systems. *Acta Agriculturae Scandinavica, Section B—Soil & Plant Science*, 66, 602-612.

Norby, R.J., Ledford, J., Reilly, C.D., Miller, N.E. and O'Neill, E.G., 2004. Fine-root production dominates response of a deciduous forest to atmospheric CO_2 enrichment. *Proceedings of the national Academy of Sciences*, 101, 9689-9693.

Nykanen, H., Alm, J., Lang, K., Silvola, J., and Martikainen, P., 1995. Emissions of CH_4, N_2O and CO_2 from a Virgin Fen and a Fen Drained for Grassland in Finland. *Journal of Biogeography*, 22, 351-357.

Ollinger, S.V., Aber, J.D., Reich, P.B. and Freuder, R.J., 2002. Interactive effects of nitrogen deposition, tropospheric ozone, elevated CO_2 and land use history on the carbon dynamics of northern hardwood forests. *Global Change Biology*, 8, 545-562.

Oomes, M. J. M., Olff, H., and Altena, H. J., 1996. Effects of vegetation management and raising the water table on nutrient dynamics and vegetation change in a wet grassland. *Journal of Applied Ecology*, 576-588.

Osanai, Y., Tissue, D.T., Bange, M.P., Anderson, I.C., Braunack, M.V. and Singh, B.K., 2017. Plant-soil interactions and nutrient availability determine the impact of elevated CO_2 and temperature on cotton productivity. *Plant and Soil*, 410, 87-102.

Ostberg, S., Schewe, J., Childers, K. and Frieler, K., 2018. Changes in crop yields and their variability at different levels of global warming. *Earth System Dynamics*, 9, 479-496.

Ostrowska, A. and Porębska, G., 2015. Assessment of the C/N ratio as an indicator of the decomposability of organic matter in forest soils. *Ecological Indicators*, 49, 104-109.

Page, S.E., Morrison, R., Malins, C., Hooijer, A., Rieley, J.O. and Jauhiainen, J., 2011. Effects of peat surface greenhouse gas emissions from oil palm plantations in Southeast Asia. White Paper Number 15. Indirect Effects of Biofuel Production Series. International Council on Clean Transportation, Washington.

Palmer, M., Howard, T., Tinker, J., Lowe, J., Bricheno, L., Calvert, D., Edwards, T., Gregory, J., Harris, G., Krijnen, J. and Pickering, M., 2018. UKCP18 marine report. Met Office Hadley Centre. Last retrieved on 30.07.2019 from https://www.metoffice.gov.uk/pub/data/weather/uk/ukcp18/science-reports/UKCP18-Marine-report.pdf

Pang, J., Zhu, J.G., Xie, Z.B., Liu, G., Zhang, Y.L., Chen, G.P., Zeng, Q. and Cheng, L., 2006. A new explanation of the N concentration decrease in tissues of rice (*Oryza sativa* L.) exposed to elevated atmospheric pCO_2. *Environmental and Experimental Botany*, 57, 98-105.

Parish, F., Sirin, A., Charman, D., Joosten, H., Minayeva, T., Silvious, M. and Stringer, L., 2008. Assessment on Peatlands, Biodiversity and Climate Change: Main Report. Global Environment Centre, Kuala Lumpur and Wetlands International, Wageningen.

Pazzagli, P.T., Weiner, J. and Liu, F., 2016. Effects of CO_2 elevation and irrigation regimes on leaf gas exchange, plant water relations, and water use efficiency of two tomato cultivars. *Agricultural Water Management*, 169, 26-33.

Peacock, M., Gauci, V., Baird, A.J., Burden, A., Chapman, P.J., Cumming, A., Evans, J.G., Grayson, R.P., Holden, J., Kaduk, J. and Morrison, R., 2019. The full carbon balance of a rewetted cropland fen and a conservation-managed fen. *Agriculture, Ecosystems & Environment*, 269, 1-12.

Pedersen, E.P., Michelsen, A. and Elberling, B., 2018. In situ CH_4 oxidation inhibition and 13 CH_4 labeling reveal methane oxidation and emission patterns in a subarctic heath ecosystem. *Biogeochemistry*, 138, 197-213.

Peltoniemi, K., Laiho, R., Juottonen, H., Bodrossy, L., Kell, D.K., Minkkinen, K., Mäkiranta, P., Mehtätalo, L., Penttilä, T., Siljanen, H.M. and Tuittila, E.S., 2016. Responses of methanogenic and methanotrophic communities to warming in varying moisture regimes of two boreal fens. *Soil Biology and Biochemistry*, 97, 144-156.

Petersen, S.O., Hoffmann, C.C., Schäfer, C.M., Blicher-Mathiesen, G., Elsgaard, L., Kristensen, K., Larsen, S.E., Torp, S.B. and Greve, M.H., 2012. Annual emissions of CH_4 and N_2O, and ecosystem respiration, from eight organic soils in Western Denmark managed by agriculture. *Biogeosciences*, 9, 403-422.

Poyda, A., Reinsch, T., Kluß, C., Loges, R. and Taube, F., 2016. Greenhouse gas emissions from fen soils used for forage production in northern Germany, *Biogeosciences*, 13, 5221-5244.

Preston, M.D., Eimers, M.C., and Watmough, S.A., 2011. Effect of moisture and temperature variation on DOC release from a peatland: conflicting results from laboratory, field and historical data analysis. *Science of The Total Environment*, 409, 1235-1242.

Pritchard, S.G. and Rogers, H.H., 2000. Spatial and temporal deployment of crop roots in CO_2-enriched environments. *The New Phytologist*, 147, 55-71.

Pulford, I.D. and Tabatabai, M.A., 1988. Effect of waterlogging on enzyme activities in soils. *Soil Biology and Biochemistry*, 20, 215-219.

Qiu, Q., Wu, L., Ouyang, Z., Li, B. and Xu, Y., 2016. Different effects of plant-derived dissolved organic matter (DOM) and urea on the priming of soil organic carbon. *Environmental Science: Processes & Impacts*, 18, 330-341.

R Development Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Radville, L., McCormack, M.L., Post, E., and Eissenstat, D.M., 2016. Root phenology in a changing climate. *Journal of Experimental Botany*, 67, 3617-3628.

Regina, K., Pihlatie, M., Esala, M. and Alakukku, L., 2007. Methane fluxes on boreal arable soils. *Agriculture, Ecosystems & Environment*, 119, 346–352.

Regina, K., Sheehy, J. and Myllys, M., 2015. Mitigating greenhouse gas fluxes from cultivated organic soils with raised water table. *Mitigation and Adaptation Strategies for Global Change*, 20, 1529–1544.

Ren, B., Dong, S., Zhao, B., Liu, P. and Zhang, J., 2017. Responses of nitrogen metabolism, uptake and translocation of maize to waterlogging at different growth stages. *Frontiers in Plant Science*, 8, 1216.

Renger, M., Wessolek, G., Schwarzel, K., Sauerbrey, R. and Siewert, C., 2002. Aspects of peat conservation and water management. *Journal of Plant Nutrition and Soil Science*, 165, 487–493.

Renou-Wilson, F., Barry, C., Müller, C., and Wilson, D., 2014. The impacts of drainage, nutrient status and management practice on the full carbon balance of grasslands on organic soils in a maritime temperate zone. *Biogeosciences*, 4361.

Richter, G.M. and Semenov, M.A., 2005. Modelling impacts of climate change on wheat yields in England and Wales: assessing drought risks. *Agricultural Systems*, 84, 77-97.

Richter, G.M., Qi, A., Semenov, M.A. and Jaggard, K.W., 2006. Modelling the variability of UK sugar beet yields under climate change and husbandry adaptations. *Soil Use and Management*, 22, 39-47.

Rinne, J., Riutta, T., Pihlatie, M., Aurela, M., Haapanala, S., Tuovinen, J.P., Tuittila, E.S. and Vesala, T., 2007. Annual cycle of methane emission from a boreal fen measured by the eddy covariance technique. *Tellus B: Chemical and Physical Meteorology*, 59, 449-457.

Riutta, T., Laine, J., and Tuittila, E.S., 2007. Sensitivity of CO_2 exchange of fen ecosystem components to water level variation. *Ecosystems*, 10, 718-733.

Rodeghiero, M., Heinemeyer, A., Schrumpf, M. and Bellamy, P., 2009. Determination of soil carbon stocks and changes. (In: Soil Carbon Dynamics: An Integrated Methodology, pp. 49-75. (Eds. W.L. Kutsch, M. Bahn and A. Heinemeyer) Cambridge University Press, Cambridge.

Rood, S.B., Nielsen, J.L., Shenton, L., Gill, K.M. and Letts, M.G., 2010. Effects of flooding on leaf development, transpiration, and photosynthesis in narrowleaf cottonwood, a willow-like poplar. *Photosynthesis research*, 104, 31-39.

Rubol, S., Silver, W.L. and Bellin, A., 2012. Hydrologic control on redox and nitrogen dynamics in a peatland soil. *Science of the Total Environment*, 432, 37-46.

Ruiz-Vera, U.M., Siebers, M.H., Jaiswal, D., Ort, D.R. and Bernacchi, C.J., 2018. Canopy warming accelerates development in soybean and maize, offsetting the delay in soybean reproductive development by elevated CO_2 concentrations. *Plant, Cell & Environment*, 41, 2806-2820.

Rustad, L.E.J.L., Campbell, J., Marion, G., Norby, R., Mitchell, M., Hartley, A., Cornelissen, J. and Gurevitch, J., 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, 126, 543-562.

Rydin, H. and Jeglum, J.K., 2006. The Biology of Peatlands. Oxford University Press. New York.

Saarnio, S., Wittenmayer, L., and Merbach, W., 2004. Rhizospheric exudation of *Eriophorum vaginatum* L. - potential link to methanogenesis. *Plant and Soil*, 267, 343-355.

Sage, R.F. and Kubien, D.S., 2007. The temperature response of C_3 and C_4 photosynthesis. *Plant, Cell & Environment*, 30, 1086-1106.

Šantrůčková, H., Kaštovská, E., Kozlov, D., Kurbatova, J., Livečková, M., Shibistova, O., Tatarinov, F. and Lloyd, J., 2010. Vertical and horizontal variation of carbon pools and fluxes in soil profile of wet southern taiga in European Russia. *Boreal Environment Research*, 15, 357–369.

Sardans, J., Grau, O., Chen, H.Y., Janssens, I.A., Ciais, P., Piao, S. and Peñuelas, J., 2017. Changes in nutrient concentrations of leaves and roots in response to global change factors. *Global Change Biology*, 23, 3849-3856.

Satapathy, S.S., Swain, D.K., Pasupalak, S. and Bhadoria, P.B.S., 2015. Effect of elevated [CO_2] and nutrient management on wet and dry season rice production in subtropical India. *The Crop Journal*, 3, 468-480.

Schoen, V. and Lang, T., 2016. Horticulture in the UK: potential for meeting dietary guideline demands. Last retrieved on 30.07.2019 from http://openaccess.city.ac.uk/id/eprint/14319

Schott, L., Lagzdins, A., Daigh, A.L.M., Craft, K., Pederson, C., Brenneman, G. and Helmers, M.J., 2017. Drainage water management effects over five years on water tables, drainage, and yields in southeast Iowa. *Journal of Soil and Water Conservation*, 72, 251-259.

Schrier-Uijl, A.P., Kroon, P.S., Hendriks, D.M.D., Hensen, A., Van Huissteden, J., Berendse, F. and Veenendaal, E.M., 2014. Agricultural peatlands: towards a greenhouse gas sink–a synthesis of a Dutch landscape study. *Biogeosciences*, 11, 4559-4576.

Schrier-Uijl, A.P., Kroon, P.S., Leffelaar, P.A., Van Huissteden, J.C., Berendse, F. and Veenendaal, E.M., 2010. Methane emissions in two drained peat agro-ecosystems with high and low agricultural intensity. *Plant and Soil*, 329, 509–520.

Schwalm, M., and Zeitz, J., 2015. Concentrations of dissolved organic carbon in peat soils as influenced by land use and site characteristics - A lysimeter study. *Catena*, 127, 72-79.

Seale, R., 1975. Soils of the Ely district (sheet 173) (Soil Survey of Great Britain (England and Wales). Memoirs). Harpenden (Rothamsted Experimental Station, Harpenden, Herts.): Soil Survey.

Segers, R., 1998. Methane production and methane consumption: a review of processes underlying wetland methane fluxes. *Biogeochemistry*, 41, 23-51.

Sepulveda-Jauregui, A., Hoyos-Santillan, J., Martinez-Cruz, K., Anthony, K.M.W., Casper, P., Belmonte-Izquierdo, Y. and Thalasso, F., 2018. Eutrophication exacerbates the impact of climate warming on lake methane emission. *Science of the Total Environment*, 636, 411-419.

Serrano-Silva, N., Sarria-Guzmán, Y., Dendooven, L. and Luna-Guido, M., 2014. Methanogenesis and methanotrophy in soil: a review. *Pedosphere*, 24, 291-307.

Setter, T.L., Waters, I., Sharma, S.K., Singh, K.N., Kulshreshtha, N., Yaduvanshi, N.P.S., Ram, P.C., Singh, B.N., Rane, J., McDonald, G. and Khabaz-Saberi, H., 2008. Review of wheat improvement for waterlogging tolerance in Australia and India: the importance of anaerobiosis and element toxicities associated with different soils. *Annals of Botany*, 103, 221-235.

Shabala, S., 2011. Physiological and cellular aspects of phytotoxicity tolerance in plants: the role of membrane transporters and implications for crop breeding for waterlogging tolerance. *New Phytologist*, 190, 289-298.

Shaw, S.B., Mehta, D. and Riha, S.J., 2014. Using simple data experiments to explore the influence of non-temperature controls on maize yields in the mid-West and Great Plains. *Climatic Change*, 122, 747-755.

Shen, Y. and Benner, R., 2018. Mixing it up in the ocean carbon cycle and the removal of refractory dissolved organic carbon. *Scientific Reports*, 8, 2542.

Sheppard, S.K., Beckmann, M. and Lloyd, D., 2007. The effect of temperature on methane dynamics in soil and peat cores: Calculations from membrane inlet mass spectrometry. *Canadian Journal of Soil Science*, 87, 11-22.

Shurpali, N.J., Hyvönen, N.P., Huttunen, J.T., Biasi, C., Nykänen, H., Pekkarinen, N., and Martikainen, P.J., 2008. Bare soil and reed canary grass ecosystem respiration in peat extraction sites in Eastern Finland. *Tellus B: Chemical and Physical Meteorology*, 60, 200-209.

Sinsabaugh, R.L., Gallo, M.E., Lauber, C., Waldrop, M.P. and Zak, D.R., 2005. Extracellular enzyme activities and soil organic matter dynamics for Northern hardwood forests receiving simulated nitrogen deposition. *Biogeochemistry*, 75, 2.

Sionit, N., Strain, B.R. and Hellmers, H., 1981. Effects of different concentrations of atmospheric CO_2 on growth and yield components of wheat. *The Journal of Agricultural Science*, 97, 335-339.

Springob, G. and Kirchmann, H., 2003. Bulk soil C to N ratio as a simple measure of net N mineralization from stabilized soil organic matter in sandy arable soils. *Soil Biology and Biochemistry*, 35, 629-632.

Stanley, C.D. and Harbaugh, B.K., 2002. Water Table Depth Effect on Water Use and Tuber Yield for Subirrigated Caladium Production. *HortTechnology*, 12, 679-681.

Steinaker, D.F., and Wilson, S.D., 2008. Phenology of fine roots and leaves in forest and grassland. *Journal of Ecology*, 96, 1222-1229.

Stiehl-Braun, P.A, Hartmann, A.A., Kandeler, E., Buchmann, N.I.N.A. and Niklaus, P.A., 2011. Interactive effects of drought and N fertilization on the spatial distribution of methane assimilation in grassland soils. *Global Change Biology*, 17, 2629-2639.

Stitt, M. and Krapp, A., 1999. The interaction between elevated carbon dioxide and nitrogen nutrition: the physiological and molecular background. *Plant, Cell & Environment*, 22, 583-621.

Strack, M., Waddington, J.M. and Tuittila, E.S., 2004. Effect of water table drawdown on northern peatland methane dynamics: Implications for climate change. *Global Biogeochemical Cycles*, 18.

Sullivan, P.F., Arens, S.J., Chimner, R.A., and Welker, J.M., 2008. Temperature and microtopography interact to control carbon cycling in a high arctic fen. *Ecosystems*, 11, 61-76.

Susilawati, H.L., Setyanto, P., Ariani, M., Hervani, A. and Inubushi, K., 2016. Influence of water depth and soil amelioration on greenhouse gas emissions from peat soil columns. *Soil Science and Plant Nutrition*, 62, 57-68.

Szafranek-Nakonieczna, A. and Stępniewska, Z., 2015. The influence of the aeration status (ODR, Eh) of peat soils on their ability to produce methane. *Wetlands Ecological Management*, 23, 665-676.

Taft, H.E., Cross, P.A., Edwards-Jones, G., Moorhouse, E.R., and Jones, D.L., 2017. Greenhouse gas emissions from intensively managed peat soils in an arable production system. *Agriculture, Ecosystems & Environment*, 237, 162-172.

Taft, H.E., Cross, P.A., and Jones, D.L., 2018. Efficacy of mitigation measures for reducing greenhouse gas emissions from intensively cultivated peatlands. *Soil Biology and Biochemistry*, 127, 10–21.

Tang, S., Xi, L., Zheng, J. and Li, H., 2003. Response to elevated CO_2 of Indian mustard and sunflower growing on copper contaminated soil. *Bulletin of Environmental Contamination and Toxicology*, 71, 988-997.

Tarnocai, C., Canadell, J.G., Schuur, A.G., Kuhry, P., Mazhitova, G. and Zimov, S., 2009. Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biochemical Cycles*, 23, 2023.

Taub, D.R. and Wang, X., 2008. Why are nitrogen concentrations in plant tissues lower under elevated CO_2? A critical examination of the hypotheses. *Journal of Integrative Plant Biology*, 50, 1365-1374.

Thibodeaux, L.J. and Aguilar, L., 2005. Kinetics of peat soil dissolved organic carbon release to surface water. Part 2. A chemodynamic process model. *Chemosphere*, 60, 1190-1196.

Thomas, K.L., Price, D. and Lloyd, D., 1995. A comparison of different methods for the measurement of dissolved gas gradients in waterlogged peat cores. *Journal of Microbiological Methods*, 24, 191-198.

Thomas, S.M., Whitehead, D., Reid, J.B., Cook, F.J., Adams, J.A. and Leckie, A.C., 1999. Growth, loss, and vertical distribution of *Pinus radiata* fine roots growing at ambient and elevated CO_2 concentration. *Global Change Biology*, 5, 107-121.

Tian, S., Jia, Y., Ding, Y., Wang, R., Feng, R., Song, Z., Guo, J. and Zhou, L., 2014. Elevated Atmospheric CO_2 Enhances Copper Uptake in Crops and Pasture Species Grown in Copper-Contaminated Soils in a Micro-Plot Study. *CLEAN–Soil, Air, Water*, 42, 347-354.

Tiemeyer, B., Albiac Borraz, E., Augustin, J., Bechtold, M., Beetz, S., Beyer, C. and Förster, C., 2016. High emissions of greenhouse gases from grasslands on peat and other organic soils. *Global Change Biology*, 22, 4134-4149.

Tiemeyer, B. and Kahle, P., 2014. Nitrogen and dissolved organic carbon (DOC) losses from an artificially drained grassland on organic soils. *Biogeosciences*, 11, 4123-4137.

Tognoni, F., Halevy, A.H. and Wittwer, S.H., 1966. Growth of bean and tomato plants as affected by root absorbed growth substances and atmospheric carbon dioxide. *Planta*, 72, 43-52.

Trost, B., Prochnow, A., Drastig, K., Meyer-Aurich, A., Ellmer, F. and Baumecker, M., 2013. Irrigation, soil organic carbon and N_2O emissions. A review. *Agronomy for Sustainable Development*, 33, 733-749.

Tveit, A.T., Urich, T., Frenzel, P. and Svenning, M.M., 2015. Metabolic and trophic interactions modulate methane production by Arctic peat microbiota in response to warming. *Proceedings of the National Academy of Sciences*, 112, E2507-E2516.

Uddin, S., Löw, M., Parvin, S., Fitzgerald, G.J., Tausz-Posch, S., Armstrong, R., O'Leary, G. and Tausz, M., 2018. Elevated [CO_2] mitigates the effect of surface drought by stimulating root growth to access sub-soil water. *PLOS one*, 13, 0198928.

Uddling, J., Broberg, M.C., Feng, Z. and Pleijel, H., 2018. Crop quality under rising atmospheric CO_2. *Current Opinion in Plant Biology*, 45, 262-267.

Updegraff, K., Bridgham, S.D., Pastor, J., Weishampel, P., and Harth, C., 2001. Response of CO_2 and CH_4 emissions from peatlands to warming and water table manipulation. *Ecological Applications*, 11, 311-326.

Urban, J., Ingwers, M.W., McGuire, M.A., and Teskey, R.O., 2017. Increase in leaf temperature opens stomata and decouples net photosynthesis from stomatal conductance in *Pinus taeda* and *Populus deltoides x nigra*. *Journal of Experimental Botany*, 68, 1757-1767.

Usuda, H., 2004. Effects of growth under elevated CO_2 on the capacity of photosynthesis in two radish cultivars differing in capacity of storage root. *Plant Production Science*, 7, 377-385.

van Beek, C.L., Hummelink, E.W.J., Velthof, G.L. and Oenema, O., 2004. Denitrification rates in relation to groundwater level in a peat soil under grassland. *Biology and Fertility of Soils*, 39, 329-336.

van den Akker, J.J.H., Kuikman, P.J., De Vries, F., Hoving, I.E., Pleijter, M., Hendriks, R.F.A., Wolleswinkel, R.J., Simões, R.T.L. and Kwakernaak, C., 2010. Emission of CO_2 from agricultural peat soils in the Netherlands and ways to limit this emission. In Proceedings of the 13th International Peat Congress After Wise Use–The Future of Peatlands, Vol. 1 Oral Presentations, Tullamore, Ireland, 8–13 June 2008 (pp. 645-648).

van Gestel, N.C., Nesbit, A.D., Gordon, E.P., Green, C., Paré, P.W., Thompson, L., Peffley, E.B. and Tissue, D.T., 2005. Continuous light may induce photosynthetic downregulation in onion - consequences for growth and biomass partitioning. *Physiologia Plantarum*, 125, 235-246.

van Winden, J.F., Reichart, G.J., McNamara, N.P., Benthien, A. and Damsté, J.S.S., 2012. Temperature-induced increase in methane release from peat bogs: a mesocosm experiment. *PLOS one*, 7, e39614.

van Zalinge, B.C., Feng, Q., Aengenheyster, M. and Dijkstra, H.A., 2017. On determining the point of no return in climate change. *Earth System Dynamics*, 8, 707-717.

Veraart, A.J., De Klein, J.J. and Scheffer, M., 2011. Warming can boost denitrification disproportionately due to altered oxygen dynamics. *PLOS One*, *6*, 18508.

Verhoeven, J.T., Keuter, A., Van Logtestijn, R., van Kerkhoven, M.B. and Wassen, M., 1996. Control of local nutrient dynamics in mires by regional and climatic factors: a comparison of Dutch and Polish sites. *Journal of Ecology*, 647-656.

Victor, D.G. and Kennel, C.F., 2014. Climate policy: ditch the 2°C warming goal. *Nature News*, 514, p.30.

Waddington, J.M., Griffis, T.J. and Rouse, W.R., 1998. Northern Canadian wetlands: net ecosystem CO_2 exchange and climatic change. *Climatic Change*, 40, 267-275.

Wang, M., Wu, J., Lafleur, P.M., Luan, J., Chen, H., and Zhu, X., 2018. Can abandoned peatland pasture sequestrate more carbon dioxide from the atmosphere than an adjacent pristine bog in Newfoundland, Canada? *Agricultural and Forest Meteorology*, 248, 91-108.

Wang, X., Li, Y., Lu, H. and Wang, S., 2016. Combined effects of elevated temperature and CO_2 concentration on Cd and Zn accumulation dynamics in Triticum aestivum L. *Journal of Environmental Sciences*, 47, 109-119.

Wang, X., Zhou, B., Sun, X., Yue, Y., Ma, W. and Zhao, M., 2015. Soil tillage management affects maize grain yield by regulating spatial distribution coordination of roots, soil moisture and nitrogen status. *PLOS one*, 10, 0129231.

Watson, A., Stephen, K.D., Nedwell, D.B. and Arah, J.R., 1997. Oxidation of methane in peat: kinetics of CH_4 and O_2 removal and the role of plant roots. *Soil Biology and Biochemistry*, 29, 1257-1267.

Wei, H., Guenet, B., Vicca, S., Nunan, N., Abdelgawad, H., Pouteau, V., Sshen, W. and Janssens, I.A., 2014. Thermal acclimation of organic matter decomposition in an artificial forest soil is related to shifts in microbial community structure. *Soil Biology & Biochemistry*, 71, 1-12.

White-Monsant, A.C., Clark, G.J., Chuen, M.N.K. and Tang, C., 2017. Experimental warming and antecedent fire alter leaf element composition and increase soil C:N ratio in sub-alpine open heathland. *Science of the Total Environment*, 595, 41-50.

Wickland, K.P. and Neff, J.C., 2008. Decomposition of soil organic matter from boreal black spruce forest: environmental and chemical controls. *Biogeochemistry*, 87, 29-47.

Wildlife Trust Countryside Centre, 2019. Holme Fen. Last retrieved on 30.07.2019 from http://www.greatfen.org.uk/visit/places/HolmeFen

Wilson, D., Farrell, C.A., Fallon, D., Moser, G., Müller, C. and Renou-Wilson, F., 2016. Multiyear greenhouse gas balances at a rewetted temperate peatland. *Global Change Biology*, 22, 4080-4095.

Wolfe, D.W., Gifford, R.M., Hilbert, D. and Luo, Y., 1998. Integration of photosynthetic acclimation to CO_2 at the whole-plant level. *Global Change Biology*, 4, 879-893.

Wong, S.C., 1990. Elevated atmospheric partial pressure of CO_2 and plant growth. *Photosynthesis Research*, 23, 171-180.

Worrall, F. and Burt, T.P., 2007. Trends in DOC concentration in Great Britain. *Journal of Hydrology*, 346, 81-92.

Worrall, F., Burt, T. and Adamson, J., 2004a. Can climate change explain increases in DOC flux from upland peat catchments? *Science of the Total Environment*, 326, 95-112.

Worrall, F., Burt, T.P., Rowson, J.G., Warburton, J. and Adamson, J.K., 2009. The multi-annual carbon budget of a peat-covered catchment. *Science of the Total Environment*, 407, 4084-4094.

Worrall, F., Burt, T. and Shedden, R., 2003. Long term records of riverine dissolved organic matter. *Biogeochemistry*, 64, 165-178.

Worrall, F., Davies, H., Bhogal, A., Lilly, A., Evans, M., Turner, K., Burt, T., Barraclough, D., Smith, P. and Merrington, G., 2012. The flux of DOC from the UK - predicting the role of soils, land use and net watershed losses. *Journal of Hydrology*, 448, 149-160.

Worrall, F., Harriman, R., Evans, C.D., Watts, C.D., Adamson, J., Neal, C., Tipping, E., Burt, T., Grieve, I., Monteith, D. and Naden, P.S., 2004b. Trends in dissolved organic carbon in UK rivers and lakes. *Biogeochemistry*, 70, 369-402.

Wösten, J.H.M., Ismail, A.B. and van Wijk, A.L.M., 1997. Peat subsidence and its practical implications: a case study in Malaysia. *Geoderma*, 78, 25–36.

Wullschleger, S.D., Norby, R.J. and Gunderson, C.A., 1992. Growth and maintenance respiration in leaves of *Liriodendron tulipifera* L. exposed to long-term carbon dioxide enrichment in the field. *New Phytologist*, 121, 515-523.

Wurr, D.C.E., Hand, D.W., Edmondson, R.N., Fellows, J.R., Hannah, M.A. and Cribb, D.M., 1998. Climate change: a response surface study of the effects of CO_2 and temperature on the growth of beetroot, carrots and onions. *The Journal of Agricultural Science*, 131, 125-133.

Xu, M., Peng, F., You, Q., Guo, J., Tian, X., Xue, X., and Liu, M. 2015. Year-round warming and autumnal clipping lead to downward transport of root biomass, carbon and total nitrogen in soil of an alpine meadow. *Environmental and Experimental Botany*, 109, 54-62.

Xu, X., Huang, G., Sun, C., Pereira, L.S., Ramos, T.B., Huang, Q. and Hao, Y., 2013. Assessing the effects of water table depth on water use, soil salinity and wheat yield: Searching for a target depth for irrigated areas in the upper Yellow River basin. *Agricultural Water Management*, 125, 46-60.

Xue, Q., Zhu, Z., Musick, J.T., Stewart, B.A. and Dusek, D.A., 2003. Root growth and water uptake in winter wheat under deficit irrigation. *Plant and Soil*, 257, 151-161.

Yamakawa, Y., Saigusa, M., Okada, M. and Kobayashi, K., 2004. Nutrient uptake by rice and soil solution composition under atmospheric CO_2 enrichment. *Plant and Soil*, 259, 367-372.

Yang, G., Chen, H., Wu, N., Tian, J., Peng, C., Zhu, Q., Zhu, D., He, Y., Zheng, Q. and Zhang, C., 2014. Effects of soil warming, rainfall reduction and water table level on CH_4 emissions from the Zoige peatland in China. *Soil Biology and Biochemistry*, 78, 83-89.

Yang, Y., Luo, Y., Lu, M., Schädel, C. and Han, W., 2011. Terrestrial C:N stoichiometry in response to elevated CO_2 and N addition: a synthesis of two meta-analyses. *Plant and Soil*, 343, 393-400.

Yin, H., Xiao, J., Li, Y., Chen, Z., Cheng, X., Zhao, C. and Liu, Q., 2013. Warming effects on root morphological and physiological traits: the potential consequences on soil C dynamics as altered root exudation. *Agricultural and Forest Meteorology*, 180, 287-296.

Yiqi, L. and Zhou, X., 2006. Soil Respiration and the Environment. Academic Press, London. pp 328

Yordanova, R.Y., Uzunova, A.N. and Popova, L.P., 2005. Effects of short-term soil flooding on stomata behaviour and leaf gas exchange in barley plants. *Biologia Plantarum*, 49, 317-319.

Yrjälä, K. I. M., Tuomivirta, T., Juottonen, H., Putkinen, A., Lappi, K., Tuittila, E. S. and Fritze, H., 2011. CH_4 production and oxidation processes in a boreal fen ecosystem after long-term water table drawdown. *Global Change Biology*, 17, 1311-1320.

Yu, C.Q., Shen, Z.X., Zhang, X.Z., Sun, W. and Fu, G., 2014. Response of soil C and N, dissolved organic C and N, and inorganic N to short-term experimental warming in an alpine meadow on the Tibetan Plateau. *The Scientific World Journal*, 2014.

Zhang, Y. and Marschner, P., 2016. Nutrient availability, soil respiration and microbial biomass after the second residue addition are influenced by the C/N ratio of the first residue added, but not by drying and rewetting between residue amendments. *European Journal of Soil Biology*, 77, 68-76.

Zhang, Z., Qiao, M., Li, D., Yin, H. and Liu, Q., 2016. Do warming-induced changes in quantity and stoichiometry of root exudation promote soil N transformations via stimulation of soil nitrifiers, denitrifiers and ammonifiers? *European Journal of Soil Biology*, 74, 60-68.

Ziegler, S.E., Billings, S.A., Lane, C.S., Li, J. and Fogel, M.L., 2013. Warming alters routing of labile and slower-turnover carbon through distinct microbial groups in boreal forest organic soils. *Soil Biology and Biochemistr*y, 60, 23-32.

Zimov, S.A., Schuur, E.A. and Chapin III, F.S., 2006. Permafrost and the global carbon budget. *Science*, 312, 1612-1613.

Zona D., Janssens I.A., Gioli B., Jungkunst H.F., Camino Serrano M., Ceulemans R., 2013. N_2O fluxes of a bio-energy poplar plantation during a two years rotation period. *Global Change Biology Bioenergy*, 5, 536-547.

Annexe 1: Abbreviations

aCO_2 – Ambient CO_2

DOC – Dissolved organic carbon

eCO_2 – Elevated CO_2

ER – Ecosystem Respiration

GHG – Greenhouse gases

GPP – Gross Primary Production

GWP – Global Warming Potential

LAI – Leaf Area Index

NEE – Net Ecosystem Exchange

NUE – Nitrogen Use Efficiency

PAR – Photosynthetically Active Radiation

POC – Particulate organic carbon

RCP – Representative Concentration Pathway

Rh – Soil Respiration

RUE – Radiation Use Efficiency

SOC – Soil organic carbon

SOM – Soil organic matter

WUE – Water Use Efficiency

Annexe 2: Soil extractions of 'pseudo-total' heavy metals by aqua regia digestion

Source: Department of Animal and Plant Science, University of Sheffield

Reagents:

- 3:1 v/v HCl : HNO_3
- Hydrochloric acid 12 M (37 % HCl, ρ=1.19 g/cm3) - trace element analyses
- Nitric acid 15.8 M (65-67% HNO_3, ρ=1.42 g/cm3) - trace element analyses
- Hydrogen peroxide (30%) - trace element analyses

Materials:

- Soil samples (air-dried and ball-milled auger soil samples < 2 mm)
- Dispenser
- Glass digestion tubes and watch glasses
- Digestion system (Block)
- Vortex
- Whatman filter paper (n. 41 or 42)
- 50 ml centrifuge tubes
- Funnels
- 15 ml centrifuge tubes for ICP-MS analysis

Procedure:

- Weight 0.25 g (+/- 0.02 g) of soil and place it in the digestion tubes (Note the exact weight).
- Add at maximum 3 ml of H_2O_2 30%.
- Add 2 ml of HNO_3 65-67%.
- Leave it overnight.
- The next morning boil the samples at 120°C (increase the temperature gradually).
- Add 6 ml of HCl 37%.
- Digest for about 90-120 minutes at 120/130°C. Increase the temperature gradually (50 >70 >90 °C...).
- After the digestion let to cool it down for at least 1 h.
- Fill the tube up to 50 ml with UPW (Ultra Pure Water).
- Filter through grade 41/42 Whatman filter into 50 ml centrifuge tubes
- Dilute the samples.
- Dilution: add 9 ml of UPW to 1 ml of digested solution (10 times dilution factor).

Some safety and quality measures:

Always work with eye protection (PPE) and under the fume cupboard, change the gloves every 2h, always decant the acid into the water.

Always use UPW to prepare all solutions.

Always acid bathe all glassware and tubes the day before, wash them with UPW, then air dry.

Always add 1 or 2 blanks and 1 or 2 soil reference materials for each batch.