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Impacts of warming, drought and sea level rise on ombrotrophic peatlands

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Thesis Abstract

Northern ombrotrophic peatlands have sequestered and stored carbon in their soils over millennia, during a period of relatively stable, long term climatic conditions. Global climate change, including increasing mean annual temperatures, increased frequency of summer droughts and increased likelihood of seawater flooding poses threats to the balance of conditions that peatlands require to continue performing these ecosystem services.

This research was based at Cors Fochno lowland raised bog in Ceredigion, West Wales, UK. As a temperate maritime peatland on the edge of the ecosystem's bioclimatic envelope and lying within one km of the coastline of the Irish Sea, it offers an ideal opportunity to investigate peatland responses to the impacts of climate change; in particular responses to seawater flooding, increased mean annual temperatures and drought events.

In laboratory conditions, two *Sphagnum* moss species (*Sphagnum pulchrum* and *Sphagnum cuspidatum*) were immersed in seawater for 72 hours, in otherwise optimised growth conditions, in order to identify photosynthetic responses to inundation. Measurements following removal of the seawater showed both species' photosynthetic rates declined sharply following treatment, with no signs of recovery.

When in-situ peat monoliths with intact vegetation were flooded with seawater, the rate of net ecosystem CO_2 exchange was reduced, and methane emissions to the atmosphere were also inhibited. Damage to vegetation was evident, resulting in an overall reduction of both CO_2 and CH_4 exchange from the peatland to the atmosphere.

In another long-term field experiment manipulating peatland plots with passive warming and summer droughts, short-term carbon dioxide gas flux responses were measured during an enforced drought. Net ecosystem exchange flux rates were significantly lower in combined warm and drought treatments than controls, indicating that the longer-term effects of the treatment may lead to a shift from a CO_2 sink to a CO_2 source.

This body of work provides new data for a baseline of peatland and *Sphagnum* responses to seawater inundation, adding to the developing body of evidence on combined temperature and hydrology impacts on carbon gas fluxes, which can aid in the development of management policies to mitigate the negative impacts of climate change.

Chapter 1

Introduction

1.1 Climate change

Climate change is a term used to define changes in long term weather and temperature patterns, in particular driven by changes in land use, the proliferation of pollutants and increases in the concentrations of greenhouse gases (Stocker et al, 2013; Wong, 2015).

Greenhouse gases are gaseous compounds in the atmosphere which allow long wave radiation to pass through the Earth's atmosphere and warm the surface. However, when the re-radiated energy, now at a shorter wavelength, reaches the atmosphere on its way back out into space, the greenhouse gases can absorb and re-emit some of the energy back towards the surface, known as radiative forcing (Wong, 2015).

The main greenhouse gas by concentration in the atmosphere is water vapour, but other gases contribute to the effect, with differing degrees of impact. These gases are given a weighting, known as global warming potential (GWP) which is measured against carbon dioxide (CO_2) as a reference. For example, methane (CH_4) has a GWP 28 times that of CO_2 over a 100-year atmospheric life cycle (Stocker et al, 2013).

As naturally occurring compounds, the carbon based gases CO_2 and CH_4 are part of the global carbon cycle that involves the movement of carbon from one reservoir to another via numerous pathways and processes, including fast and slow cycles. The slow cycle involves geological processes such as rock formation and weathering, and moves through the environment over millions of years. The fast carbon cycle involves the cycling of carbon through organic matter. Plants and phytoplankton uptake atmospheric carbon dioxide (CO_2) in the process of photosynthesis, producing sugar used for energy and growth, and oxygen as a waste product. During the burning of carbohydrates for energy by microbes, plants, by animals which have eaten the plants (or animals which have eaten the animals which have eaten the plants), or by fire, CO_2 is returned to the atmospheric pool. These cycles can be very short (hours-days) or last centuries and can be affected by external drivers such as solar energy inputs, orbital shifts, vegetation clearance, soil loss and fossil fuel burning (Wong, 2015). In certain circumstances, the return of CO_2 from the biological to atmospheric pool can be delayed due to conditions, which inhibit the decay of organic matter, such as those found in peatlands. However, the functions of such CO_2 sinks are also dependent upon climatic conditions, and changes in these can lead to disruption of ecosystem services such as carbon sequestration and storage.

Since the 18th century, when an increase in the use of fossil fuels led to the development of industrial processes and human population increases, there have been significant effects on the Earth's atmosphere. An estimated 555 Pg of carbon have been released to the atmosphere from fossil fuel and land use emissions between 1750 and 2011, resulting in an observed increase of atmospheric CO_2 concentration of 40% from 278 ppm to 411 ppm (Stocker et al, 2013; NOAA, 2019). The concentration of CH_4 has increased by a factor of 2.5 since preindustrial times, from 0.7 ppm in 1750 to 1.8 ppm in 2011 (Stocker et al, 2013). Anthropogenic sources of CH_4 are over twice the size of natural sources, at 574 Tg CH_4 y^{-1} compared to 238 Tg CH_4 y^{-1} (Stocker et al, 2013; Van Amstel 2012).

The effect of increases in atmospheric concentrations of CO_2 and CH_4 has been an increase in the global mean surface temperature (GMST), with the period 1983–2012 very likely the warmest 30-year period of the last 800 years in the northern hemisphere (Stocker et al, 2013). Predictions for future GMST trends indicate temperatures will continue to rise through the 21st century (between 0.3°C to 0.7°C) with projected increases in the duration, intensity and spatial extent of heat waves and warm spells for the near term from around the mid-21st century (Stocker et al 2013). The years 2008 to 2017 were on average 0.8°C warmer than the 1961-1990 period, and predictions at the lower end of the high emissions scenarios suggest a 0.9°C increase in summer temperatures by 2070 (Lowe et al 2018).

Droughts, defined here as lack of rainfall and low soil water availability, have been more prevalent in the 20th than the 19th century, associated with temperature increase in the 20th century. These may be one-off events, lasting weeks to months, or may be more severe lasting decades such as the 1890-1910 major drought in the UK (Marsh et al 2007). Since the beginning of records in the UK (1766), precipitation volumes in summer have decreased, with predictions of changes in summer precipitation for the UK in 2070 between -47% and +2% in high CO_2 emissions scenario, (Lowe et al 2018).

Global mean sea levels fluctuate due to changes in plate tectonics and isostatic rebound, and also the volume of water present in the oceans, which is associated with glacial development and melting processes and the thermal expansion of water. Since 1901, not only have sea levels increased, but they have also done so at an increasing rate with the estimated global mean sea level rise for 2081-2100 between 0.26 and 0.82 m (Stocker et al 2013); whilst European mean sea level is expected to increase to between

0.53-0.77 m by 2100, with an associated 25 cm average increase in extreme sea levels along European coasts by 2050 (Vousdoukas et al 2017).

How these changes in climate will interact with peatlands is an area of intense research focus, due to the loss of peatlands for peat harvesting and changes in land use, and the loss of carbon sequestration and carbon storage services provided by peatlands, as well as their emissions to the atmosphere.

1.2 Peatlands

A peatland is an ecosystem where carbon dioxide, assimilated from the atmosphere into plant biomass, is incompletely mineralised back into its gaseous form and is incorporated into wet soils with high carbon content. This results in soils that are naturally wet and high in carbon, defined as histosols (WRB 2015), but commonly known as peat.

Peat soils are found in conditions where, at their time of formation, plant biomass production rates exceeded those of microbial decomposition rates. These conditions may occur due to physical characteristics (e.g. sediment deposition above organic matter in coastal saline marshes) or climatic, where precipitation and temperature interact to produce suitable peat forming conditions.

Ombrotrophic peatlands have become isolated from underlying sources of water and nutrients, which they receive solely from the atmosphere, hence the descriptive term ombrotrophic (cloud fed) although nutrients may have been derived from the substrate during earlier stages of their development (Clymo 1983). The defining characteristics of where an ombrotrophic peatland may form are high annual rainfall rates which exceed losses through evapotranspiration, low mean annual temperatures, high moisture and low variability between seasons (Lindsay, 1995).

Peatlands are dominated by hydrological process. They are wet habitats with water tables general just below the surface, and thus many vegetation species are tolerant of periodically anaerobic conditions and have developed mechanisms that enable them to thrive in saturated soil conditions. Other species of vegetation, and microbial communities, are obligate wetland or even anaerobic in character, and their fitness suffers when water levels decrease, and thus oxygen availability increases.

As the natural state of a lowland raised bog is a water table at the surface, it seems reasonable to assume that short term (days-weeks) of freshwater flooding would have little negative impact upon a peatland, and as such there is little published work in this area.

In the northern hemisphere, peatlands began their development about 10,000 years ago, and approximately 15,000 years ago in the southern hemisphere (MacDonald et al 2006), and now cover approximately 4 $\times 10^6$ km^2, approximately 3 % of the earth's total land surface area (Bain et al., 2011; Xu et al 2018). They are mostly found in the northern hemisphere between 50 and 70 degrees latitude, especially in Russia, Canada and North America, (Moore, 2002; Yu et al 2010).

Peatlands in an active state (known as mires) accumulate carbon from the atmosphere and store it in their soils. However, the condition of peatlands varies greatly. For example, of the estimated 600,000 km^2 of peatland in Europe, only approximately 50 % is active mire i.e. peat forming (Tannenberger et al 2017). Damage or changes to the conditions in which peat is formed or stored may result in the release of carbon from peatlands, changing them from carbon sinks to carbon sources (Rydin and Jeglum 2013).

Aerobic bacteria decompose organic material in their metabolic processes, but peat soils may develop in the anaerobic conditions that inhibit decomposition processes (Clymo & Hayward 1982). Peat soils are generally characterised by high water tables and may be 85 % water by volume (Evans and Warburton 2007). In a raised peatland, for example, the oldest (i.e. lowest) peat in a vertical profile may be dominated by nutrient demanding species, only later succeeded by species more commonly associated with ombrotrophic (i.e. low nutrient availability) species as the peat surface gradually loses contact with subsurface nutrient sources. This condition is fulfilled when the water table is high within the soil column, due to a combination of an imbalance between water inputs and outputs, and low hydraulic conductivity. Impermeable substrates can slow the vertical infiltration of water through soils, and so pools in depressions in the landscape are ideal initiation points for the development of peatlands. Raised peatlands develop in a process known as paludification, where vegetation encroaches upon a body of water from the edges, eventually covering the surface (Schumann & Joosten, 2008). This may initially result in the creation of a more nutrient rich and vegetation diverse fen habitat, due to nutrient supply from rock minerals and groundwater, as well as the atmosphere. Over time, as dead vegetation builds up in the water, the competitive ability of fen vegetation declines in favour of species which are better adapted to lower nutrient inputs as the fen peat creates a physical barrier between plant roots and underlying nutrient sources (Lindsay 1995; Rydin and Jeglum 2013). Bryophytes of the family *Sphagnaceae* are particularly well adapted in taking advantage of this situation, and thus the peatland, although initially minerogenic and minerotrophic, becomes ombrotrophic (Van Breemen 1995).

The effects *Sphagnum* has upon the chemistry of water, soil quality and water tables have led to its definition as an ecosystem engineer, whose presence or absence affects the entire ecosystem (Van Breemen 1995). They grow from their upper tip section (capitula), whilst the lower sections of the plant become functionally dead from about 10 cm below the capitula from where they begin to decompose (Clymo 1983). Depending on their growth form and ecological niche, they may grow in dense hummocks, in looser lawns or more open pools, dependent upon their water requirements and ability to tolerate and recover from desiccation (Rydin & Jeglum; 2013). Sphagna differ from vascular plants in that they do not possess a vascular system for the transportation of nutrients, water and metabolic products through the plant. Instead, they absorb water and nutrients directly through their cuticle from the atmosphere. This thus restricts them to environments where there is frequent precipitation and high humidity, but also allows them to intercept nutrients on the surface before they fall into the rooting zone of vascular species (Rydin & Jeglum 2013). During nutrient uptake, *Sphagna* exude hydrogen ions, resulting in the acidification of the surrounding waters (Clymo, 1964). *Sphagnum* also has low decomposability properties (Turetsky 2003; Van Breemen 1995).

The peatland surface is uneven, generally defined into low lying, continuously wet pools, slightly raised lawns, and exposed hummocks dominated by *Sphagnum* mosses, with occasional patches of bare peat (Rydin & Jeglum, 2013). Vascular species include rushes, sedges, shrubs and trees, though these may be sparsely distributed and restricted to drier areas.

Below the vegetated surface is the acrotelm, a zone 20-30 cm deep, characterised by fluctuating water tables, active rooting structures of vascular plants, and more decomposable plant material (Lindsay, 1995). In this zone, water may flow laterally as well as vertically as the peat is not compacted enough to limit flow (Rydin & Jeglum, 2013). Within this layer, oxygen is available to microbes for use in metabolic processes. This results in the production of CO_2 as a waste product. Below the acrotelm lies the catotelm, which is a zone of low hydraulic conductivity, and temperature, and almost constantly waterlogged and dominated by anaerobic microbial communities. Below the peatland is the substrate, often of an impermeable character (e.g. clay or marl deposits).

Along with many wetland types, peatlands provide ecosystem services including water management, natural resources (food, medicines, building materials, agriculture, fuel), and cultural services (e.g., recreation, education) (TEEB 2013). Of particular importance is their ability to sequester atmospheric carbon within their soils (between 16-88 Gt C every 1000 years, (Yu et al 2012), and store this carbon over millennia, with an estimated 455-600 Gt of carbon in peat soils globally (Gorham, 1991).

Of the CO_2 utilised for photosynthetic processes by peatland plants, some of the carbon produced naturally leaves the system as gas (CO_2, CH_4) or transported by water (dissolved or particulate carbon), but a proportion remains in a partially decomposed state, which contributes to the formation of peat soils. This fraction becomes buried as the *Sphagnum* vegetated surface grows vertically, and decomposition rates decrease in depth due to anaerobicity, lower temperatures and the reduced quality of the carbon substrate (Moore, 2002).

In dry, aerobic conditions, often found in the acrotelm, peat may be oxidised by bacteria and returned to the atmosphere as CO_2. When anaerobic conditions prevail, for example deeper within the peat column or during periods of high water tables, methane is produced by groups of anaerobic microorganisms (Euryarchaeota, Domain Archaea) in a food web utilising the carbon rich substrate, of which methanogens are the final link (Boon et al, 2014). Methane in peatlands is released to the atmosphere via ebullition, diffusion or plant mediated via aerenchymous structures (Couwenburg 2009; Greenup et al 2000). However, some of the methane produced in peatlands is oxidised to CO_2 by methanotrophs close to the surface, which utilise CH_4 as a substrate in metabolism (Boon et al 2014). Whilst diffusion is the slowest pathway to the atmosphere, it does allow for interaction with methanotrophs, whilst aerenchyma and ebullition pathways bypass the methanotrophic layer.

Different greenhouse gases can be compared in terms of their effect on global warming by an index known as Global Warming Potential (GWP). The baseline value of 1 is the GWP of CO_2, chosen because CO_2 has a long residence time in the atmosphere. Other gases have multiples of this values, for example, Methane (CH_4) has a GWP of 28 (over a 100-year period), whilst Nitrous Oxide has a GWP of 265 over the same timescale (Stocker et al 2013). In the short term, wetlands, including peatlands, may appear to be sources of atmospheric greenhouse gases and thus contributors to climate warming due to their GWP from emissions of CO_2 and CH_4. However, over longer timescales (centuries to millennia), they become net CO_2 sinks, and thus mitigate against climate warming (Mitsch et al 2012; Whiting & Chanton 2001).

1.3 Peatland responses to temperature and drought

Temperature has a strong relationship with both ecosystem respiration and gross primary productivity in *Sphagnum* peatlands, with both increasing with increasing temperatures (Chivers et al 2009; Juszczak et al 2013; Lafleur et al, 2005; Lindroth et al 2007; Updegraff et al 2001). Increases in mean annual temperature can lead to an increase in *Sphagnum* photosynthesis rates as long as water content is maintained (Haraguchi and Yamada 2011). In *Sphagnum* dominated ombrotrophic peatlands in the northern hemisphere, ambient air temperatures are often below the optimum for *Sphagnum* primary productivity. Optimum temperatures for photosynthesis (assuming optimum water content and light levels) are between 20 and 35°C in warm and cool temperate mires (Haraguchi & Yamada, 2011; Harley et al., 1989), although there is often an associated rise in CO_2 respiration rates. These responses are species specific, with some species attaining their highest photosynthesis rates at 25°C (Fukuta et al, 2012). Above 35 °C cell damage may occur (Balagurova et al, 1996; Gerdol & Vicentini, 2011).

Ecosystem respiration rates (combined autotrophic and heterotrophic respiration) are likely to increase in warmer conditions. However, the combined effect of increased respiration and primary productivity may result in an overall increase in the net ecosystem exchange rates of a peatland, increasing the CO_2 sink function. For example, Lindroth et al (2007) found productivity responded more strongly than respiration to temperature across a range of northern peatlands.

However, droughts may minimise or even reverse any benefits in carbon sequestration due to increased productivity rates. Drought conditions result in both the desiccation of the surface vegetation and lowering of the water table depth. As *Sphagnum* plants become desiccated as water content decreases, both autotrophic respiration and primary productivity decline as photosynthetic rates fall (Robroek et al 2007). This results in an overall reduction in primary productivity, which reduces the net ecosystem exchange (Helfter 2015; Lund 2012). As the water tables lowers, more peat is exposed to aerobic conditions, allowing increased respiration of soil carbon by aerobically obligate bacteria, reducing further the net ecosystem exchange of the ecosystem (Blodau et al 2004). The overall effect in drought years may be the shift of the peatland from a carbon sink to a carbon source, although this may depend on the duration and season of a drought (Lund 2012). Sustained lowered water table may encourage the increase/succession of vascular species cover that can affect the carbon balance of a bog (Kuiper et al 2013; Ward et al 2013).

1.4 Peatland responses to seawater flooding

Global mean sea levels fluctuate due to changes in plate tectonics & isostatic rebound, and also the volume of water present in the oceans, which is associated with glacial development and melting processes and the thermal expansion of water Since 1901, not only have sea levels increased, but they have also done so at an increasing rate with the estimated global mean sea level rise for 2081-2100 range between 0.26 and 0.82m (Stocker et al 2013); whilst European mean sea level is expected to increase to between 0.53-0.77 m by 2100, with an associated 25 cm average increase in extreme sea levels along European coasts by 2050 (Vousdoukas et al 2017).

There is limited data on the distribution and extent of coastal peatlands globally, or even in the UK which are subject to seawater flooding. Whittle & Gallego-Sala (2016) identified 145,000 km^2 of peatlands globally below 5 m elevation, of which 11,500 km^2 are ombrotrophic peatlands. The combined threats of sea level rise; estimated at between 0.5-1.4 m globally by 2100 above 1990 levels (Rahmstorf, 2007) and an increase in the frequency and intensity of extreme storm and high tide events (Stocker et al 2013; Woth et al 2006) is a major concern for the management of coastal habitats, especially where inland migration of the habitat is not possible.

On average, seawater contains 35 parts per thousand (ppt) of salts (35 g l^{-1}), chemically dominated by sodium (Na) and chloride ions (Cl). The presence of saline water is detrimental to the health of the majority of plant species on earth (Flowers et al 1977). Osmosis leads to the concentration of Na and Cl salts in the tissues of plants, causing cell lysis (Volkmar et al 1998, Yadav et al 2011). However, plants that are adapted to saline habitats have evolved characteristics that enable them to withstand continuous or periodical saline conditions. These include the partitioning of salts in specialised compartments, the exuding of salts through tissues, or avoidance of salt uptake (Munns 2002; Munns and Tester 2008). These plants can also exist in freshwater contexts, however, the energetic costs of producing and maintaining tissues specifically for dealing with saline conditions, puts them at a competitive disadvantage in non-saline habits, and they are generally outcompeted.

Mosses have been the focus of only a few studies investigating responses to seawater, though they are present in saline habitats (Callaghan and Farr, 2018; Sabovljevic & Sabovljevic, 2007). They have been found in saline conditions over 20,000 mg L^{-1} (approximately equivalent to 20 ppt, or 32 mS/cm) and certain species found to be capable of photosynthesising after 24 hours of immersion in seawater, though at a reduced rate (Garbary et al 2008). Differences have been found between moss species in their ability to tolerate exposure to seawater, including the regulation of intracellular ion concentrations, photosynthesis rates, and chlorophyll fluorescence values (Bates, 1976; Bates & Brown 1974, 1975; Bates et al 2009; Boerner and Forman, 1975; Pouliot et al 2012).

No studies were found which involved *Sphagnum* responses to seawater exposure as *Sphagnum* is generally absent from saline habitats, although communities may develop where the saline influence is weakest. For example, along a transect running inland from the coastline of the west coast of Scotland, Whittle and Gallego-Sala (2016) found *Sphagnum* present at approximately 750 m from the coast, where inundation by seawater did not occur. In the Baltic Sea the small islands near Stockholm provide a habitat for Sphagnum even just metres from the sea (Sundberg et al, 2006).

In other experiments, salinity in the form of only NaCl in road de-icing salts may give insights into potential responses. NaCl at concentrations of up to 1500 mg L^{-1}

(approximately 1.5 ppt or 2.9 mS/cm) have been used, intended to isolate the individual strength of effects of Na^+ or Cl^- upon *S. recurvum* growth in length, biomass production and overall mortality or survival, due to road salt runoff. Wilcox (1984) found that whilst the NaCl concentrations were themselves non-lethal towards *Sphagnum recurvum* in treatments of up to 45 days, growth in length and biomass were both negatively affected at all concentrations used, with Cl found to be the greater inhibitor in terms of biomass production. A stimulatory effect upon biomass production was found at 500 mg L^{-1} NaCl. A similar effect was found by Pouliot et al (2012) in *S. warnstorfii* when low concentrations of NaCl (100 mg L^{-1}) led to an increase in innovation production (new shoots or capitula) of over seven days.

In the field, Wilcox and Andrus (Wilcox & Andrus, 1987) found, in a peatland which had been subject to road de-icing salts at measured concentrations of up to 800 mg L^{-1} NaCl (1.5 mS/cm), only six *Sphagnum* species were present after five years of recovery out of a previously recorded 16 species. Mortality from salt inundation at low concentrations appeared to be from physical breakdown of the plants due to salt encrustation rather than ionic effects. Seawater however has a more complex chemistry than de-icing salts that can interact with the effects of Na and Cl. For example, the presence of Ca ions in seawater has been found to reduce intracellular K loss and the influx of Na and Mg in a coastal moss *Grimmia maritima*, following immersion in artificial seawater concentrations similar to those found in natural seawater (Bates and Brown 1974); a related species (*Grimmia pulvinata*, an inland moss) did not display a similar ability to control cation concentrations.

In conditions of repeated seawater flooding, a gradient from salt marsh vegetation to ombrotrophic bog vegetation may develop (Whittle and Gallego-Sala, 2016).

Alternatively, if the seawater flooding is sustained, a halophytic vegetation community may completely replace the ombrotrophic community. Along the western Ireland Atlantic coastline, Cott et al (2012; 2013) found salt marsh communities overlying peat derived from blanket peatlands, but with a vegetation community distinct from both the original peatland type and salt marshes on sand or mud substrates. The concern for peatlands close to coastlines is that the inland margins have often been the focus of development, drainage or harvesting, thus the remaining area of such peatlands is restricted, and no inland expansion is possible, particularly where infrastructure has been placed.

Saline tolerant plants (halophytes) may survive and thrive while saline conditions persist, outcompeting non-halophyte (glycophytes) vegetation in saline conditions, but if conditions return to lower salinities, they may themselves be outcompeted by the glycophytes (Wetzel, Kitchens, Brush, & Dusek, 2004). Experiments investigating the survival of freshwater marsh vegetation exposed to brackish saline conditions (14-15 ppt) led to the death of almost all the surface vegetation, but recovery of some aspects of the freshwater vegetation community was achievable with the loss of some species, in salinity levels above initial pre-treatment conditions (Flynn et al, 1995). Furthermore, the presence or absence of neighbours may be an interacting factor in survival time in saline conditions. In a reciprocal transplant experiment, Engels and Jenson (2010) found interspecific competition had the greater effect upon survival of saline tolerant plants in freshwater conditions, whilst salinity concentrations were more important for freshwater plants in salt-water conditions.

No published studies were found investigating the effects of seawater flooding on carbon gas fluxes, specifically the movement of carbon dioxide (CO_2) and methane (CH_4)

between the atmospheric pool and ombrotrophic peatlands. A limited number of studies have been conducted on freshwater wetlands, particularly those with a salinity gradient.

In a meta-analysis of methane fluxes from a variety of marshes ranging from freshwater to salt marsh, Poffenbarger et al (2011) identified a negative relationship between pore water salinity and methane fluxes. The strongest conclusion was that in studies where salinity inputs were greater than 18 ppt, CH_4 fluxes to the atmosphere were reduced.

Short term, laboratory studies suggest that the addition of seawater to peat soils results in the suppression of CH_4 effluxes due to the suppression of methanogenesis in favour of sulphate reduction (Chambers et al 2011; Chambers et al 2014; Weston 2006). However, potential CH_4 emissions from shallow soils taken from a tidal freshwater marsh exposed to seawater treatments over 3.5 years was higher than controls (Neubauer at al 2013). As sulphate reduction rates increase, and methane production rates decrease in the presence of NaCl or seawater, so CO_2 production increases (Chambers et al 2011, Chambers et al 2014; Weston et al 2006).

1.5 Research aim & objectives

The aim of this thesis is to define and quantify the gaseous carbon responses of peatlands to seawater inundation, increased mean annual temperatures and summer droughts.

Despite the ecosystem engineer status ascribed to *Sphagnum* mosses in ombrotrophic peatlands, no published evidence was found relating to *Sphagnum* physiological responses to seawater inundation. The first objective of this thesis is to assess how the photosynthetic characteristics of *Sphagnum* respond to seawater flooding in controlled conditions.

Although work has been conducted into peatland responses to seawater flooding, the research has focussed on freshwater wetlands, which have bio-chemical conditions distinct from ombrotrophic peatlands. The second objective of this thesis is to measure the CO_2 and CH_4 gas flux responses of ombrotrophic peatlands to seawater flooding in field conditions.

It is unclear from the literature to what extent summer droughts in warmer conditions will affect CO_2 fluxes in peatlands, and whether any changes will affect the ecosystem service of carbon sequestration and storage they currently provide. The third objective of the thesis is to quantify changes in the rate of peatland CO_2 gas fluxes during a summer drought in raised temperatures compared to controls.

1.6 Site description

In this study the focus will be upon ombrotrophic peatlands (also known as bogs). The site used is an estuarine raised bog on the west coast of Wales called Cors Fochno (Borth Bog; Fig 1.1). It is adjacent to the Irish Sea, and has a seven-meter depth of peat with development stretching over 5000 years (Countryside Council for Wales 2011). It is bounded by the coastal village of Borth, the river Leri and its estuary to the north, the Pwl Du to the south, and hills to the east. The centre of the active raised bog is approximately 2 km from the coastline from which flooding is predicted (DEFRA, 2006; Robins et al., 2011; Fig 1.2). With an area of 653 ha, it is designated as a Special Area of Conservation, Site of Special Scientific Interest and Natural Nature Reserve, and part of a UNESCO biosphere reserve. It contains both active raised bog and degraded raised bog, and has a complex history of human interventions, including mining, drainage for agriculture and peat harvesting.

Vegetation on the central dome is dominated by Sphagnum mosses, particularly nationally scarce species such as *Sphagnum austinii* and *Sphagnum pulchrum*, sedges and shrubs. These species contribute to the National Vegetation Classification (NVC) community descriptors M1 and M2 which are *Sphagnum* dominated bog pool communities, and M3, M18, M19 and M20 vascular plant communities, all of which are associated with active raised mires (Elkington et al 2001).

The river Leri is raised above the surrounding peatlands by peat bunds which form the banks. During high tides, and particular astronomical spring tides or storms, seawater flows into the Leri via the junction with the river Dovey. Current projections of flooding (Environment Agency 2013) suggest that the majority of the ombrotrophic peatland may be subject to freshwater flooding, whilst saline flooding will be restricted to areas adjacent to the Dovey river or the coastline (fig. 1.2). However, failure or overtopping of the banks of the Leri during periods when the salinity levels are raised may lead to the flooding of the adjacent peatlands with seawater, thus the estimate in figure 1.2 of potential saline flooding area may be an underestimate.

Fig 1.1 Cors Fochno (Borth Bog). The outline describes approximately the peatland extent including both active and degraded bog. At the top of the image (north) lies the River Leri, to the left of the image (west) is the Irish Sea. (Image courtesy of Google Maps 2019 https://www.google.com/maps).

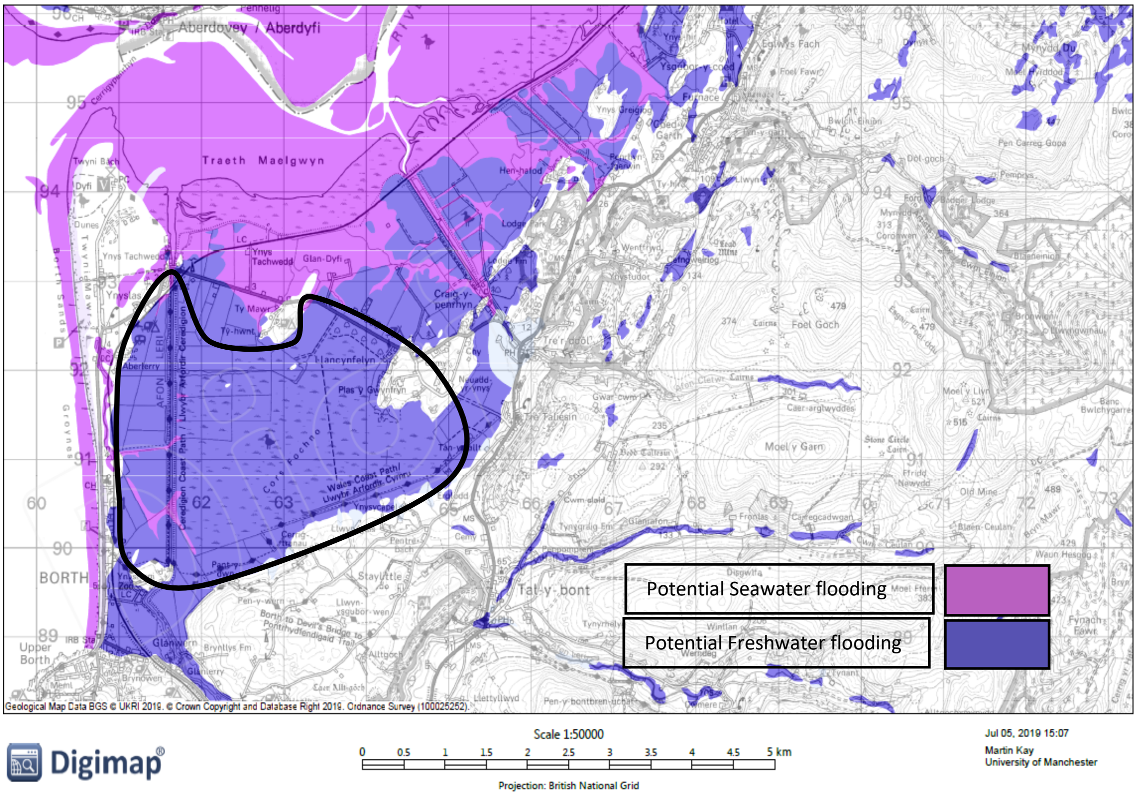


Fig 1.2 Projected extent of flooding onto peatland (general area outlined in black) due to potential seawater flooding (purple) and freshwater flooding (blue). (Image courtesy of https://digimap.edina.ac.uk/

Chapter 2

Photosynthetic responses of two *Sphagnum* species to seawater flooding

2.1 Abstract

Sphagnum bryophytes play a vital role as ecosystem engineers in the development and maintenance of ecosystem functions in ombrotrophic peatlands, particularly carbon storage and CO_2 sequestration. Predicted sea level rise and increases in storm surge frequency are likely to affect freshwater coastal peatlands, but the potential impacts of these events are poorly understood. This paper describes how the physiology of two *Sphagnum* species of contrasting ecological niches responded to seawater exposure in the laboratory. After a 72 hr immersion in seawater, rates of photosynthesis and chlorophyll fluorescence values declined in both species. The effects were strongest in *S. cuspidatum*, with *S. pulchrum* demonstrating greater tolerance. Neither species recovered to pretreatment chlorophyll fluorescence values or rates of photosynthesis by the end of the experiment. We discuss the implications of these results for community composition and the potential ecosystem-scale effects of seawater flooding in ombrotrophic bogs.

2.2 Introduction

Ombrotrophic peatlands are wetland habitats where low evaporation rates and high precipitation inputs result in saturated soils with low oxygen availability, and nutrient inputs are limited to atmospheric sources, as vegetation is separated from groundwater by a peat substrate (Rydin and Jeglum, 2013). Ombrotrophic peatlands are most widely found in the northern hemisphere in regions with temperate to subarctic climates, and cover an estimated 3% of global land surface (Kaat and Joosten, 2009; Limpens et al., 2008). The acidic, waterlogged conditions limit aerobic microbial decomposer activity, resulting in the development of soils with high carbon (C) content. Over millennial timescales, peatlands are sinks for atmospheric CO_2 (Freeman et al., 2001; Rydin and Jeglum, 2013), estimated to accumulate 61-70 Tg C y^{-1}, and currently contain 473-621 Gt C, approximately a third of the world's terrestrial C pool (Gorham, 1991; Turunen et al., 2002; Yu et al., 2010).

In temperate, northern boreal and sub-arctic peatlands, key ecosystem functions, including the sequestration and storage of atmospheric CO_2, are closely associated with one family of bryophytes, the Sphagnaceae (genus *Sphagnum*) (Turetsky, 2003; Turetsky et al., 2012). As rootless, avascular species, Sphagna are at a competitive disadvantage in many terrestrial habitats, but possess properties that enable them to thrive and outcompete many vascular species in the challenging conditions of peatlands. These properties include efficient uptake of atmospherically-derived nutrients, the acidification of surrounding waters via ion exchange, and low herbivore palatability (van Breemen, 1995; Fritz et al., 2014).

When conditions become unsuitable for *Sphagnum* species to dominate, such as increases in nutrient availability, or a decrease in available water, shifts towards vascular dominated communities have been reported (Breeuwer et al., 2009; Dieleman et al., 2014; Heijmans et al., 2013). The resulting biochemical interactions between peat, surface vegetation and microbes can cause peatlands to shift from carbon sinks to sources (Kuiper et al., 2014) and potentially feedback into global C cycles (Bridgham et al., 2008; Limpens et al., 2008). Research on the impacts of global change factors such as atmospheric pollution on peatlands is reasonably well-established, but a factor which has been little-studied to date is coastal seawater flooding.

Both sea levels and storm surge events are expected to increase in their frequency and intensity in the next century (Stocker et al 2013), with impacts estimated to affect over 70% of coastal wetlands globally (Nicholls, 2004; Wong et al 2014). An estimated area of 145,000-150,000 km^{-2} of global peatland is less than 5 m elevation above sea level in areas vulnerable to coastal flooding, with 11,500 km^{-2} of this being ombrotrophic bogs (Whittle and Gallego-Sala, 2016). Although this is a small fraction of the total area of global peatlands, they contain an estimated 20.2 ± 2.5 Gt C in their soils (Henman and Poulter, 2008; Whittle and Gallego-Sala, 2016), which is almost equivalent to estimates of the UK's total peat soil C stores (Byrne et al., 2004). It is possible that a substantial, but currently unquantified, proportion of these peatlands at risk of seawater flooding will be *Sphagnum* dominated vegetation communities.

Much of the research into plant physiological responses to salinity has been undertaken in vascular plants, particularly those of economic value. The effects of exposure to salt stress (as NaCl) generally result in reduced growth rate in leaves and roots, and increased concentrations of ions in cytoplasm and cell walls, which may ultimately lead to the death of plants (Munns, 2002; Volkmar et al., 1998). However, some vascular species also possess mechanisms that may aid in their tolerance of salinity, including the evasion, compartmentalisation or exclusion of Na^+ and Cl^- ions from tissues as evident in halophytic species (Munns and Tester, 2008), particularly those that frequent coastal habitats, for example *Salicornia* species of the Chenopodiaceae family (Lonard et al., 2012).

As most bryophytes lack the physical structures of vascular species, which contribute to tolerance or resistance of salinity exposures, it might be assumed that mosses are more susceptible to the effects of salinity. Indeed, documented effects of seawater or salinity treatments in mosses report: reductions in chlorophyll fluorescence values (Bates et al., 2009); an increase in intracellular Na^+, Cl^- and loss of K^+ ions (Bates, 1976); a reduction in chlorophyll content and photosynthetic capacity (Bates and Brown, 1975); and an increase in mortality (Wilcox, 1984); all similar salinity stress responses displayed by many non-halophytic vascular species. However, there is evidence of variability between species, with some mosses shown to be more tolerant of higher salinity concentrations, both in laboratory and natural environmental settings (Bates & Brown, 1974; Bates et al., 2009; Boerner and Forman, 1975; Callaghan and Farr, 2018)

Responses to salinity as NaCl in *Sphagnum* are negative even at low concentrations, with increases in mortality and reductions in biomass reported (Pouliot et al., 2013; Wilcox and Andrus, 1987), as well as interspecific differences in the ability of *Sphagnum* species to recolonise bogs after road salt inundation (Wilcox and Andrus 1987). However, as seawater contains a complex mix of ions, which have been shown to have differential effects upon moss physiology when present or absent in treatments (Bates and Brown, 1974), there is a requirement for research focusing specifically on seawater impacts. An estimated 11,500 km^2 of ombrotrophic bogs are dominated by *Sphagnum* species, and given the importance of *Sphagnum* in these habitats, it is surprising there are no published studies on *Sphagnum* responses to seawater, as this knowledge could inform strategic planning for coastal management, the calculation of regional greenhouse gas budgets, and direct local site management and conservation practices.

Therefore, given the importance of *Sphagnum* in ombrotrophic bogs, and their role in ecosystem carbon storage and sink functions, knowledge of the physiological responses of *Sphagnum* species to seawater flooding will contribute to improved predictions of responses of peatland carbon pools and vegetation communities to climate change. In this study, we addressed the response of *Sphagnum* photosynthetic parameters to short-term seawater inundation focussing on two *Sphagnum* species; *Sphagnum cuspidatum* and *Sphagnum pulchrum*, both of section Cuspidata, but occupying different niches within the same habitat, in order to address the hypotheses that;

1. seawater flooding will reduce *Sphagnum* CO_2 uptake,
2. increase CO_2 efflux, and
3. reduce chlorophyll fluorescence values.

2.3 Methods and materials

2.3.1 Experimental design

Cors Fochno National Nature Reserve (OS grid reference SN 636 926; 52.503N, 4.021W) is an active lowland raised bog on the west coast of Wales, approximately one km inland from the high tide mark, covering an area of 6.5km^2. It has been identified as being acutely at risk of sea water incursions due to projected increased frequencies of storm surges, and net sea level rise (DEFRA, 2006; Robins et al., 2011), and has experienced seawater flooding in the recent past (M. Bailey, J. Lyons; Natural Resources Wales; pers. comm.).

Samples of two *Sphagnum* species were collected from the central dome in June 2015 and transported to the laboratory where they were kept in cool (10°C) and dark conditions for two days until preparation. *S. cuspidatum* is a very widely dispersed pioneer species, present in peatlands globally, and abundant in many peatland regions exposed to potential sea level rise impacts. *S. pulchrum* is a less widespread, later successional species, contributing more strongly than *S. cuspidatum* to peat deposition, with a distribution that suggests the possibility of a preference for maritime sites, conceivably linked with salt tolerance in the UK due to their maritime distribution (Atherton et al 2010). For each species, approximately 350 individual plants were selected for similarity of capitula size, colour and general appearance, and cut to a length of two cm. The selected plants were randomly assigned to treatments and measurement type. An individual plant was considered as a single capitula, associated stem, and pendant foliage.

All plants were placed into a growth chamber (Weiss-Gallenkamp Fitotron) five days before treatments commenced in order to acclimatise to optimum conditions for photosynthesis identified by pre-trials. These conditions were 16:8 hours light to dark ratio with temperatures of 20°C and 10°C respectively and a two-hour ramp time between night and day conditions in order to approximate conditions in the field. Daytime light levels were approximately 500 μmol m^{-2} s^{-1} (±50 μmol m^{-2} s^{-1}) at the capitula surface and humidity was maintained at >90%.

Bogwater (BW) was collected from bog pools at Cors Fochno, and seawater (SW) from the adjacent coastline. Rainwater (RW) was collected on site during the period of plant collection. Water samples were kept in cool, dark conditions in the laboratory after filtration (Fisherbrand QL100 filter, 5-13µm diameter pore size). Ion content of treatment waters was analysed using a Thermo Scientific Dionex Ion Chromatograph (ICS-2000). pH and conductivity were measured using calibrated Mettler Toledo FiveEasy FE20 and FE30 models respectively.

All treatments comprised of 72 hours of inundation in either BW or SW in order to simulate a temporary flooding event, following which treatment waters were poured off. A light spray of RW was applied on a daily basis to avoid desiccation for a further eight-day recovery period, and the whole experiment lasted for 11 days. All measurements were taken between 1000 and 1600 hr. Initial baseline measurements (T0) were taken immediately prior to inundation. Measurement T1 through to T5 were taken every other day for each species following the inundation period, thus the results for both species refer to T0, though measurements began on alternate days.

2.3.2 Photosynthesis and respiration

Twenty replicate units of each species, each unit consisting of 12-15 plants, were randomly assigned to either a SW or BW treatment (i.e. 10 replicates per treatment). There was no untreated control group in this experiment. This was decided as a compromise between taking relatively frequent measurements on two species, and the time consuming nature of the measurement technique.

The plants in each replicate unit were arranged in a single layer in a 50 ml glass beaker and the replicates were placed into trays. Each tray was partially filled with BW, and covered with transparent plastic film with air holes, in order to allow light transference to the plants while maintaining high humidity levels. Just prior to measurements, the plants were lightly blotted to remove excess external water (which can act as a barrier to gas transfer) and transferred to a Parkinson Leaf Chamber with a chamber area of 6.2cm^{-2}. Measurements of photosynthesis and respiration were taken using an ADC LCA3 Portable Photosynthesis System with in-built infrared gas analyser (ADC BioScientific Ltd).

Airflow was maintained at 120 L min^{-1}, humidity at >90% and temperature at 20°C ± 0.5°C, based on published optimum temperature and light conditions for photosynthesis in temperate northern hemisphere *Sphagnum* species (Haraguchi and Yamada, 2011; Harley et al., 1989; Rice et al., 2008) and laboratory pre-trials, with reference to usual seasonal conditions at the collection site. Both photosynthesis and respiration values were recorded after five minutes in order to allow the system to equilibrate, but before signs of desiccation. A light level of 500 μmol m^{-2} s^{-1} was used for photosynthesis; respiration was then measured in the dark after a 30-minute dark adaptation period. Ambient CO_2 levels were approximately 450 ppm for all measurements.

2.3.3 Chlorophyll fluorescence measurements

Chlorophyll fluorescence measures the uptake of photons by photosystem II (PsII), which relates to the plant's potential for photosynthesis. The technique is commonly applied in measurements involving plant stress, as a decrease in PsII efficiency can indicate damage to the photosynthetic apparatus within a plant. The measures are reported as *Fv/Fm*, which range from 0-0.99, though the commonly accepted value for a healthy plant is 0.8 (Bates et al 2009; Maxwell and Johnson 2000).

Only one measurement was taken on each plant, as during trials repeatedly attaching and removing the dark adjustment clips often led to physical damage of the capitula. 120 plants were required for each species, divided into two treatments, and randomly assigned one of six measurement points (T0-T5). Treatments periods were as for photosynthesis, and each tube was covered with plastic film to maintain humidity and reduce evaporative loss.

On each measurement occasion, ten plants of each species and treatment were lightly blotted and dark adapted for ten minutes. *Fv/Fm* values were measured using a Photosynthesis Efficiency Analyser (Hansatech, King's Lynn, UK), with gain set at x10 and light intensity at 500 μmol m^{-2} s^{-1} for a duration of 1 s.

2.3.4 Data analysis

To analyse the effects of treatment and time on photosynthesis and respiration, a two-way mixed-effects ANOVA model was used, with time as a repeated measure, and treatment as the independent variable. Outliers were detected both visually and with Studentised residuals, normality was tested using Q-Q plots and Shapiro-Wilk tests, equality of covariance with Box tests (Greenhouse Geisser corrections were used if significant), sphericity with Mauchly's test and homogeneity of variances with Levene's test. Bonferroni adjusted Tukey post-hoc tests were used for analysis of pairwise differences following significant ANOVA results. Although aspects of the chlorophyll fluorescence data violated some assumptions of the statistical analysis method, non-parametric and parametric results were similar, so the results from the ANOVA model are reported. Significance was set at the 0.05 level. All data were analysed in SPSS V.21 (IBM; 2012). The micrometeorological nomenclature system was used for CO_2 fluxes, where a positive value indicates a flux from plants to the atmosphere, and a negative value indicates uptake from the atmosphere to plants.

2.4 Results

2.4.1 Chemistry and appearance

With the exceptions of PO_4^{3-} and NH_4 the SW chemistry values were orders of magnitude greater than the RW and BW, which was reflected in higher conductivity and pH, and RW was slightly higher in all chemistry values than BW, with the exception of phosphate (Table 2.1). Visually, *S. cuspidatum* plants in SW lost colouration following the 3-day SW immersion, and did not regain colour during the recovery period after the SW was drained off (Fig 2.1). *S. pulchrum* appeared visually unaffected by SW. There were no changes in the appearance of either species when treated with BW alone.

Table 2.1. Treatment water chemical analysis values for Seawater (SW), Bogwater (BW) and Rainwater (RW). Conductivity is reported in *m*S cm^{-1}; ions measured in *m*g l^{-1}).

Treatment	Cond	pH	Na^+	Cl^-	SO_4^{2-}	Mg^{2+}	Ca^{2+}	K^+	NO_3^{1-}	PO_4^{3-}	NH_4+
SW	49.4	7.07	6689	11328	1803	743	391	356	247	0	0
BW	0.01	5.65	13.02	20.63	1.15	1.57	1.50	0.62	0.15	0.3	0.04
RW	0.16	5.74	19.36	32.22	8.40	2.34	3.60	1.15	1.38	0	0.05

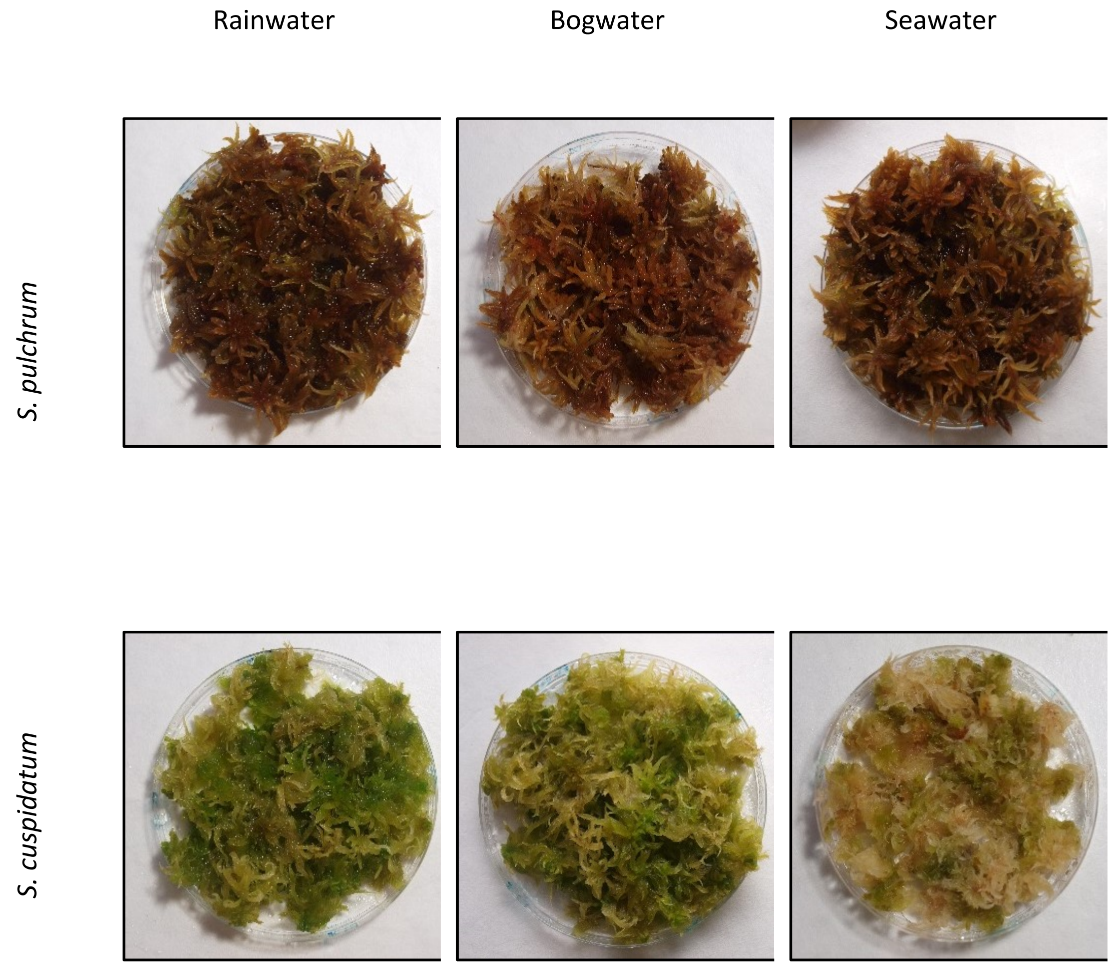


Fig 2.1. Visual appearance of treatments after 11 days, from L-R: rainwater spray, bogwater immersion followed by rainwater spray, seawater immersion followed by rainwater spray, top *S. pulchrum*, bottom *S. cuspidatum*.

2.4.2 Photosynthesis

Photosynthesis rates in *S. pulchrum* diverged significantly from baseline values in the SW treatment from T1 onwards ($F_{(1.9,17.0)} = 52.5$, $p < 0.001$) and in the BW treatment from T2 ($F_{(5,45)} = 121.3$, $p < 0.001$, Table 2.2, Fig 2.2). However, trends in photosynthesis responses differed by treatment, with CO_2 uptake in SW treatments falling to 40% of baseline by T2, whilst BW treated plants increased CO_2 uptake to a high of 160% of baseline by T3. These differences between treatments were statistically significant at all measurement times following treatment (Table 2.3, Fig 2.2). These results are qualified by a significant interaction between time and treatment ($F_{(2.85,51.3)} = 133.2$, $p < 0.001$).

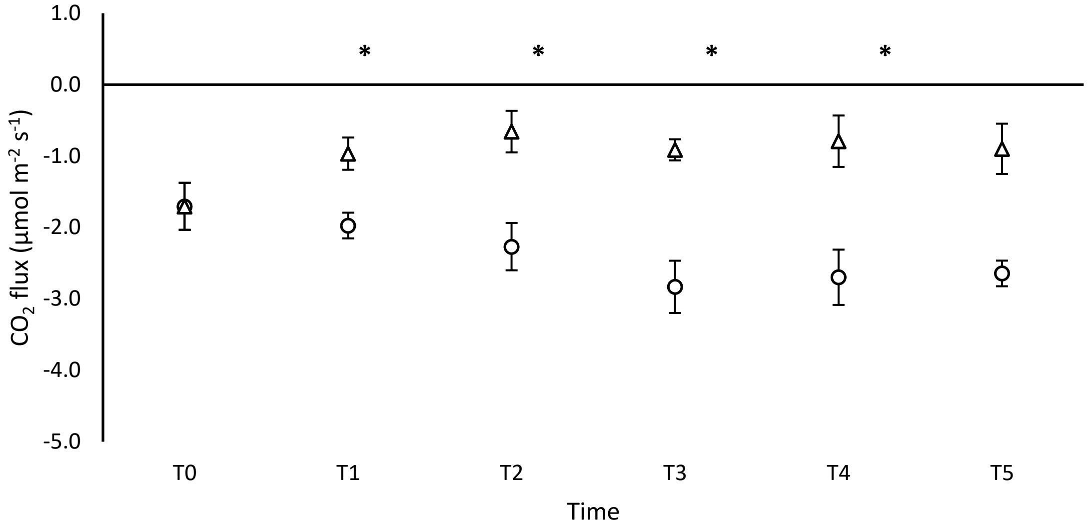


Fig 2.2. *S. pulchrum* photosynthesis fluxes, bogwater O, seawater Δ. Error bars are ±1se. Asterisk indicate statistical significance between treatments.

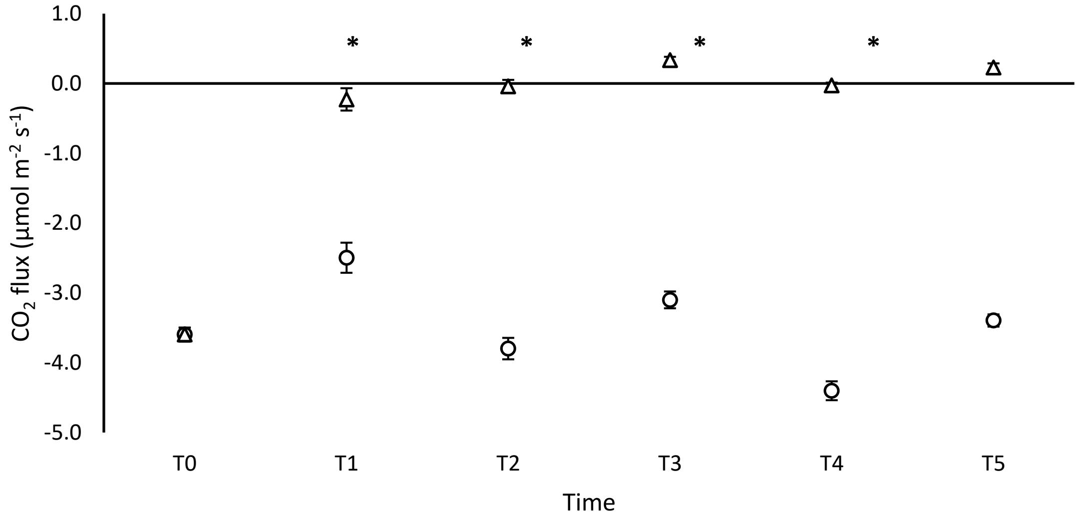


Fig 2.3. *S. cuspidatum* photosynthesis fluxes, bogwater O, seawater Δ. Error bars are ±1se. Asterisk indicate statistical significance between treatments.

Table 2.2. Pairwise comparisons between baseline and subsequent times in *S. pulchrum*. *P* values are of post-hoc Tukey HSD with Bonferroni adjustments for multiple comparisons. Significant values at the *p*≤0.05 value are highlighted in bold.

	Respiration	Photosynthesis		*Fv/Fm*	
Time	Collapsed across treatment	Bogwater	Seawater	Bogwater	Seawater
T0-T1	**0.05**	0.023	**<.001**	1.00	0.15
T0-T2	0.1	**<.001**	**<.001**	**0.01**	**0.04**
T0-T3	1.00	**<.001**	**0.002**	**0.01**	0.10
T0-T4	1.00	**<.001**	**<.001**	1.00	**0.04**
T0-T5	0.73	**<.001**	**<.001**	1.00	**0.02**

Table 2.3. Simple main effects one-way ANOVA results between treatments (df=1). Significant values at the *p*≤0.05 value are highlighted in bold. Results for *S. pulchrum* respiration are not shown as the between subject test was non-significant (see text).

	S. cuspidatum						*S. pulchrum*			
	Respiration		Photosynthesis		*Fv/Fm*		Photosynthesis		*Fv/Fm*	
Time	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
T1	0.32	.578	71.3	**<.001**	12.7	**<.002**	121.4	**<.001**	7.8	**0.012**
T2	5.38	**.032**	440.4	**<.001**	88.7	**<.001**	124.9	**<.001**	21.1	**<.001**
T3	4.46	**.049**	726.0	**<.001**	102	**<.001**	107.9	**<.001**	21.3	**<.001**
T4	8.61	**.009**	964.2	**<.001**	59.8	**<.001**	129.9	**<.001**	18.6	**<.001**
T5	10.1	**.005**	1167.4	**<.001**	47.7	**<.001**	194.5	**<.001**	15.1	**<.001**

S. cuspidatum photosynthesis fluctuated around baseline in the BW treatment, but CO_2 uptake fell to almost zero at T1 in SW, and remained near zero for the rest of the experiment, with positive values (i.e. net respiration) at T3 and T5 (Fig 2.3). Significant differences were present between baseline and subsequent values in BW from T2 onwards ($F_{(1.8,16.5)}$ = 122.6, $p < 0.001$), and in SW between baseline and post treatment from T1 onwards ($F_{(1.3,11.9)}$ = 810.4, $p < 0.001$, Table 2.4). Statistically significant differences between treatments were present from T1 onwards (Table 2.3, Fig 2.3). The results are qualified by a significant interaction between time and treatment ($F_{(1.7,31.0)}$ = 405.3, $p < 0.001$).

2.4.3 Chlorophyll fluorescence

For *S. pulchrum* there was comparatively little change over time in *Fv/Fm* values in the BW treatment (Fig 2.4) although there were statistically significant differences ($F_{(5, 45)}$ = 5.42, *p*=0.001) between baseline values and both T2 and T3 (Fig 2.4, Table 2.2). A stronger and more convincing effect was evident in the SW treatment, with significant differences ($F_{(5,45)}$ = 5.61, *p*=0.001) between baseline and T2, T4 and T5 (Table 2.2). Significant differences between treatments were found from T1 onwards (Table 2.3) with BW values consistently higher than SW (Fig 2.4). There was a statistically significant interaction between time and treatment ($F_{(2.9,52.3)}$ = 5.81, *p*=0.03).

A similar response to the *S. pulchrum* BW treatment was seen in *S. cuspidatum Fv/Fm* values, with no statistically significant differences between baseline and later measurements (Fig 2.5). However, in the SW treatment, values declined sharply from T1, with significant differences found between baseline and all subsequent values ($F_{(5,45)}$ = 14.8, *p* <0.001; Table 4). Differences between treatments were evident from T1 onwards with no sign of recovery (Fig 2.5, Table 2.3). There was a statistically significant interaction between time and treatment ($F_{(2.7,48.8)}$ = 15.1, *p* < 0.001).

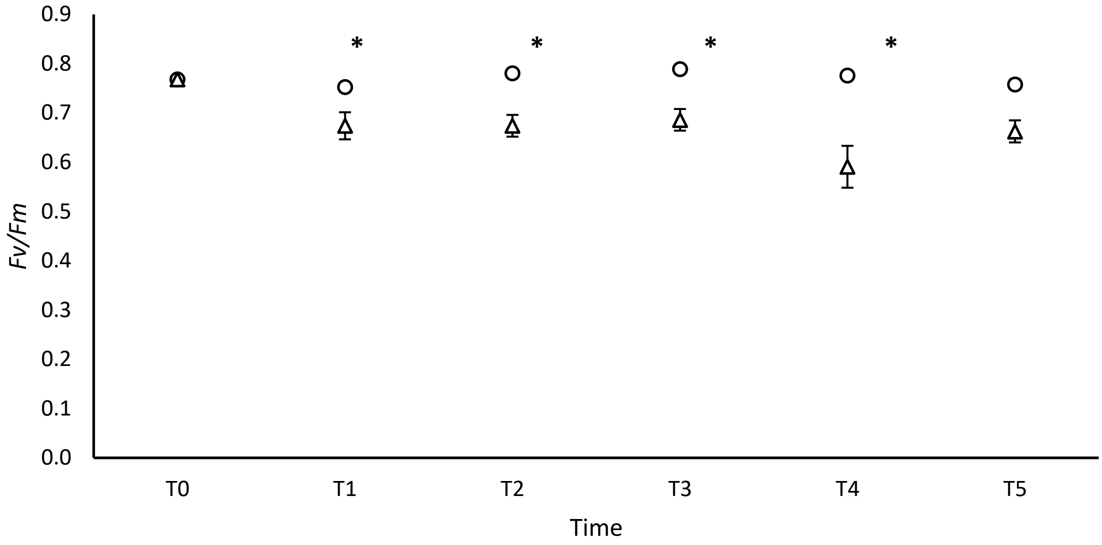


Fig 2.4. *S. pulchrum* chlorophyll fluorescence values, bogwater O, seawater Δ. Error bars are ±1se. Asterisk indicate statistical significance between treatments.

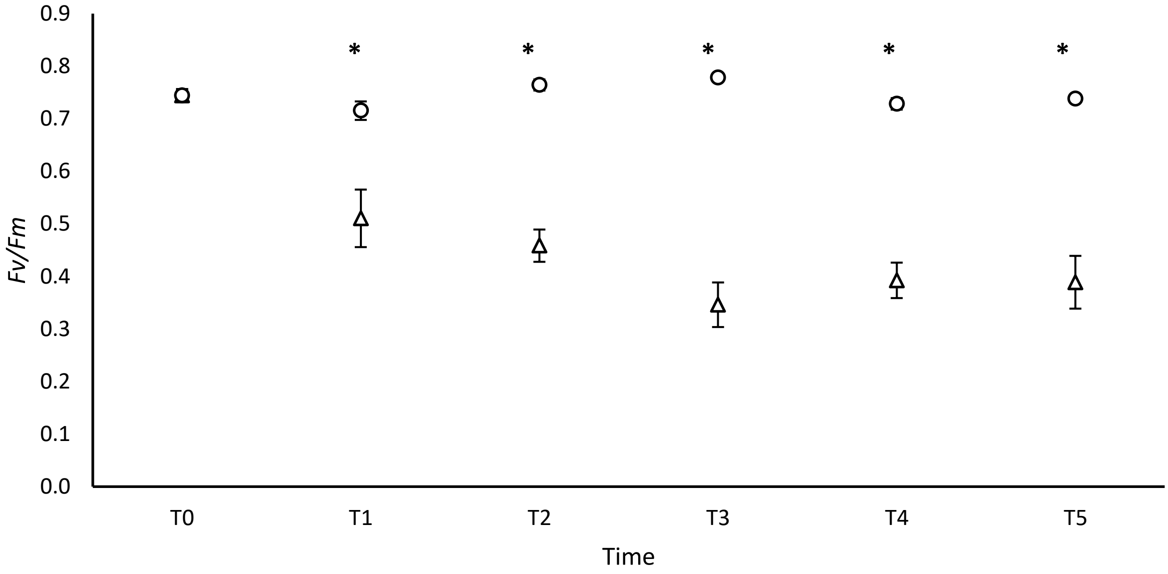


Fig 2.5. *S. cuspidatum* chlorophyll fluorescence values, bogwater O, seawater Δ. Error bars are ±1se. Asterisk indicate statistical significance between treatments.

2.4.4 Respiration

S. pulchrum respiration values remained similar to baseline during the experiment regardless of treatment (Fig 2.6), and although initially the ANOVA model suggested statistically significant differences were present between baseline and post treatment values, ($F_{(5,90)}$ = 2.37, p = 0.05), pairwise comparisons did not produce significant results for either treatment. There were no significant differences in respiration values between treatments at any time ($F_{(1,18)}$ = 3.99, p = 0.06), nor was there an interaction between treatment and time on respiration values ($F_{(5,90)}$ = 0.48, p = 0.79).

The effects of SW on *S. cuspidatum* respiration were also slight, but a significant difference between sampling occasions was found in the BW treatment ($F_{(5,45)}$ = 11.1, p <0.001), between baseline and T5 (p=0.025), but no differences between sampling occasions were found in the SW treatment ($F_{(2.6,23.3)}$ = 1.57, p = 0.23; Table 2.4, Fig 2.7). Significant differences between treatment values were found from T2 onwards (Table 2.3). However, these effects were qualified by a significant interaction between treatment and time ($F_{(3.8,67.5)}$ = 2.99, p =0.03).

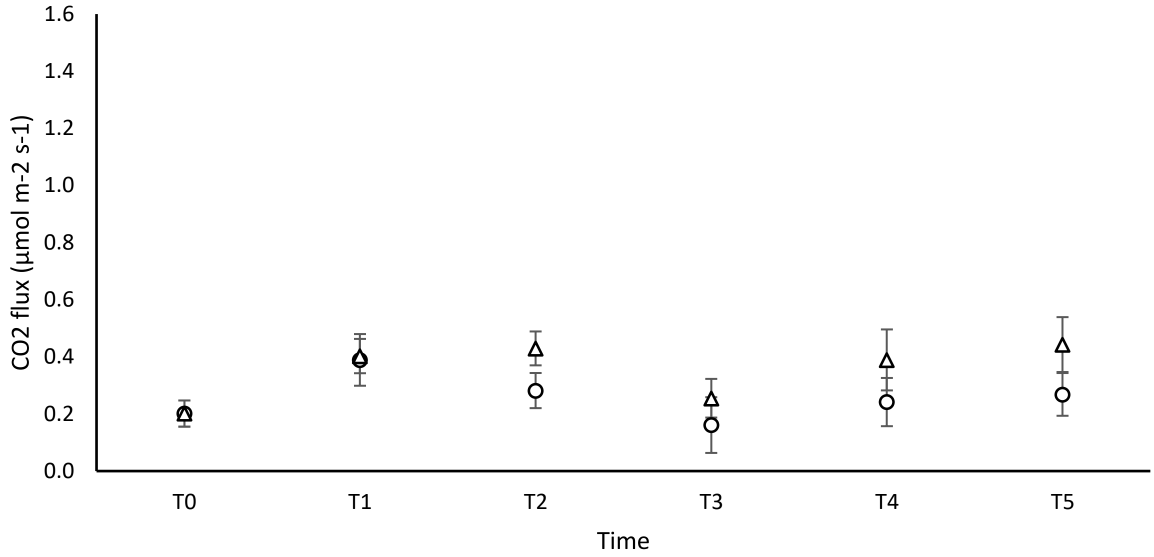


Fig 2.6. *S. pulchrum* respiration fluxes, bogwater O, seawater Δ. Error bars are ±1se.

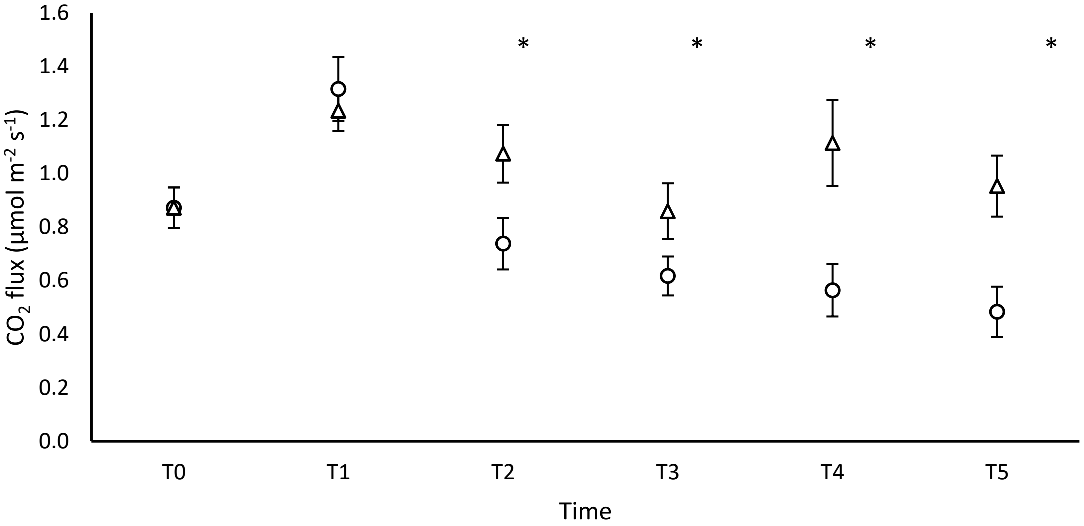


Fig 2.7. *S. cuspidatum* respiration fluxes, bogwater O, seawater Δ. Error bars are ±1se.

Asterisk indicate statistical significance between treatments.

Table 2.4. Pairwise comparisons between baseline and subsequent times in *S. cuspidatum*. *P* values are of post-hoc Tukey HSD with Bonferroni adjustments for multiple comparisons. Significant values at the *p*≤0.05 value are highlighted in bold.

	Respiration		Photosynthesis		*Fv/Fm*	
Time	Bogwater	Seawater	Bogwater	Seawater	Bogwater	Seawater
T0-T1	0.32	0.10	**<.001**	**<.001**	1.00	**0.042**
T0-T2	1.00	0.12	**<.001**	**<.001**	1.00	**<.001**
T0-T3	0.21	0.93	**<.001**	**<.001**	0.24	**<.001**
T0-T4	0.56	0.19	**<.001**	**<.001**	1.00	**<.001**
T0-T5	**0.03**	0.14	**0.005**	**<.001**	1.00	**0.001**

2.5 Discussion

The aim of this study was to identify the effects of SW flooding upon the photosynthetic characteristics of two *Sphagnum* species. In accordance with hypothesis 1, photosynthesis rates of *S. cuspidatum* were found to decrease following a three-day inundation in SW relative to both baseline values and concurrent BW treated replicates, with similar effects found for *S. pulchrum*, though this was confounded by an increase in the rate of CO_2 uptake by the BW treated samples. Chlorophyll fluorescence also responded negatively to SW treatments for both species, though respiration responses were more subdued.

As this is a novel study, there is no published literature on the effects of SW or salinity on *Sphagnum* photosynthetic physiology with which to compare these results directly. However, in inland mosses (non-*Sphagnum* species), Bates and Brown (1975) found a marked reduction in photosynthesis (measured as bicarbonate uptake) following three days' treatment, whilst deionised treated plants increased photosynthesis rates, with no evidence of recovery. This effect was similar to that seen in the *S. pulchrum* photosynthetic responses in this experiment. *Fv/Fm* responses to SW were also similar to those reported in the literature for non-*Sphagnum* mosses. Bates (2009) found *Fv/Fm* fell to approximately 57% of control values after five days of exposure to SW, similar to the *S. cuspidatum* response after seven days in this study.

In accordance with hypothesis 2, there were interspecific differences in responses to SW in both the photosynthesis and chlorophyll measurements, though not for respiration. However, whilst *S. pulchrum* did demonstrate greater resistance to the SW treatment, there was no evidence of recovery in either species. Furthermore, there were also significant differences in species' photosynthesis responses in the BW treatment. The increases in photosynthesis and respiration values in BW treated replicates may have been due to the water forming a gas transport barrier.

No salt encrustation was found in the SW treated plants in this experiment, in contrast to that reported by Wilcox (1984) which had resulted in increased mortality compared to plants that were rinsed of NaCl. It is likely that the RW spray applied daily in this experiment prevented the formation of salt crystals on the plants, and their subsequent physical deterioration. However, if weather conditions were dry following a SW flood event, mortality following salt encrustation might be a possibility.

Each species was measured on alternative days. Although this was assumed unlikely to have had a major effect upon the findings, as a detailed method was employed to avoid user error, it did preclude the inclusion of an untreated control due to the time consuming nature of photosynthesis (and respiration) measurements if two species were to be examined. The assumption was made that as the two species being used were obligate wetland species, generally existing only where water tables are only slightly below the surface, and freshwater immersion is a common occurrence for species occupying lawn and pool niches in lowland peatlands, these characteristics would allow for substitution of a BW flooded treatment for an untreated control (i.e. RW spray only). The latter treatment was considered necessary as CO_2 diffusion in water is estimated as being 10,000 times slower than in air (Clymo and Hayward, 1982), and could have effects upon CO_2 fluxes that might confound the effects of salinity.

Greater clarity with respect to the identification of effects may have been achieved with the employment of a Before-After-Control-Intervention (BACI) experimental design. This method provides the ability to distinguish between natural variation within the subjects under study, whilst simultaneously comparing differences between treatments and controls. In effect this was attempted with the T0 pre-treatment measurements on both species, but a further non-treated group (i.e not flooded with either bogwater or seawater) for each species would have been preferable.

Given the short duration of the experiment, it is difficult to infer whether a flooding event in the field would lead to the loss of either species from the vegetation community. Wilcox (1984) and Wilcox and Andrus (1987) reported that in a *Sphagnum* dominated bog, which had been affected by chronic NaCl road salt input for 17 years (Na^+ 468 mg/L, Cl^- 1215 mg/L), the most vigorous of the *Sphagnum* recolonisers was *S. fimbriatum*, which is a hummock forming species. As the authors note, this species may have succeeded due to the physical separation of the capitula from the saline water table. Although capillary action may draw saline water upwards, regeneration from fragments was strongest in *S. fimbriatum* (at 500mg/L Cl^-) than other species tested. Thus, hummock-forming species may have a competitive advantage over hollow and lawn species in the event of a saline input. However, repeated flooding events would likely lead to saline tolerant halophyte communities developing (March and Smith, 2012) as reported in coastal peatlands subjected to saline immersion (Cott et al., 2012; Cott et al., 2013).

2.6 Conclusions

This study has found that both *Sphagnum* net photosynthesis and chlorophyll fluorescence are negatively affected by short-term seawater flooding, but that there are interspecific differences in tolerance to the treatment. Future work to explore the range of tolerance between species across the ecological niche that they occupy, and responses of vascular species that inhabit these bogs would give useful information on potential community shifts in the event of seawater flooding. The duration and frequency of repetition of flooding is also likely to be of consequence, as are the seasonal conditions in which the flooding occurs. Given the complex biogeochemical interactions in bogs, and their global roles as stores and sinks of carbon from the atmosphere, future interdisciplinary work on vegetation community, microbial and greenhouse gas responses will be required to assess the full ecosystem response to seawater flooding.

Chapter 3

Peatland gaseous ecosystem CO2 and CH4 flux responses to seawater flooding

3.1 Abstract

Coastal flooding events are predicted to increase in frequency and magnitude as global mean sea levels rise, which will affect the ecosystem functions of peatlands close to coastlines. Whilst there have been numerous studies on fresh and saltwater marsh carbon dioxide (CO_2) and methane (CH_4) responses to seawater inundation, this is the first report on the responses of these greenhouse gases in ombrotrophic peatlands measured in the field.

We subjected 15 *Sphagnum* dominated plots (area of 0.078 m^2) in an ombrotrophic peatland adjacent to the Irish Sea to a one-off either 10 L of seawater, bog water or no water as a control in the spring of 2015, and took monthly field measurements of CO_2 and CH_4 gas fluxes. Both ecosystem respiration and gross primary productivity values were significantly lower in the seawater than control treatments, and CH_4 fluxes were significantly reduced in seawater treatments. *Sphagnum* vegetation was visibly affected by the seawater treatment but recovered within a year of inundation.

Our study suggests that a one-off springtime seawater flood in temperate ombrotrophic peatlands will result in the reduction of gaseous carbon exchange and cause physical damage to vegetation for at least 12 months following inundation, but subsequent signs of recovery indicate that a return to the peatland's previous state is a likely outcome

3.2 Introduction

Ombrotrophic peatbogs are characterised by their bryophyte dominated vegetation communities, low nutrient availability, acidic and anaerobic soil conditions and low rates of decomposition resulting in organic rich, peat soils. An estimated 547 Mt of carbon are stored in northern hemisphere peatlands (Yu et al 2010). Within peatlands, gaseous atmospheric CO_2 is taken up in photosynthesis, but is only partially respired back to the atmosphere by microbial and plant respiration, the remainder leaves via alternative pathways (e.g. dissolved in water leaving the system) or develops into peat soils, thus acting as a CO_2 sink over millennia. However, the anaerobic conditions found in functioning peatbogs also lead to the production of CH_4, a more potent greenhouse gas with a global warming potential 28 times that of CO_2 (over a 100-year timeframe) (Stocker et al, 2013), that can have significant short-term impacts on the carbon balance of a bog.

Rising global sea levels and predicted increases in the intensity and frequency of storm surges (Stocker et al, 2013; Vousdoukas et al, 2017; Woth et al., 2006) threaten coastal ombrotrophic peatlands that have already been severely degraded and reduced in area. Globally an estimated 11,000 km^2 of ombrotrophic peatland lie within 5 m of current sea levels (Whittle & Gallego-Sala, 2016).

Understanding on the effects of seawater flooding on the carbon flux processes of ombrotrophic peatlands is limited. Only one study on *Sphagnum* peat CO_2 and CH_4 gas responses to seawater treatment was found, in which CO_2 emissions were reduced by 60%, but there was no effect on CH_4 fluxes in a 16-week laboratory experiment (Brouns et al 2014). However, the strength of the seawater was 11% that of normal seawater, and the samples were soil only. In freshwater marsh soils, low concentrations of seawater have been found to both stimulate (Chambers et al 2011; Weston et al 2011) and also to inhibit CO_2 production (Neubauer et al 2013).

Methane emissions from wetlands have been shown to be inhibited by seawater ingressions, with significant negative correlations between the concentrations of sulphate and CH_4 (Chambers et al 2014; Wang et al 2017), particularly so when salinities reach approximately 50% of the strength of seawater (Poffenbarger et al 2011).

There is a lack of published evidence on the effects of seawater flooding on ombrotrophic bogs. Here we present the results of a field experiment detailing the responses of CO_2 and CH_4 fluxes, and vegetation characteristics to a one-off seawater flooding event in a coastal peatbog. It was hypothesised that, in the event of a one off seawater inundation in an ombrotrophic *Sphagnum* dominated peatland both CO_2 and CH_4 exchange would decrease relative to control values.

3.3 Methods

3.3.1 Study site

Cors Fochno is an estuarine lowland raised bog on the west coast of Wales (OS grid reference: SN631913; 52.503N, 4.021W, Fig. 3.1) at risk of seawater flooding due to its proximity to the Irish Sea (Robins et al., 2011; DEFRA, 2006). It is a *Sphagnum* dominated active raised bog with an area over 6.5 km^2, including the locally abundant but nationally scarce *Sphagnum pulchrum*. It is also the largest of the UK's raised bogs within an estuarine setting, part of a national nature reserve complex, and also part of the Dyfi UNESCO Biosphere Reserve.

Fig 3.1. The location map of Cors Fochno. The Irish Sea is to the left of the image. The borders of the peatlands are within 500m of the high tide mark. The experimental area is encircled in the upper right hand of the image. (Image courtesy of https://digimap.edina.ac.uk/)

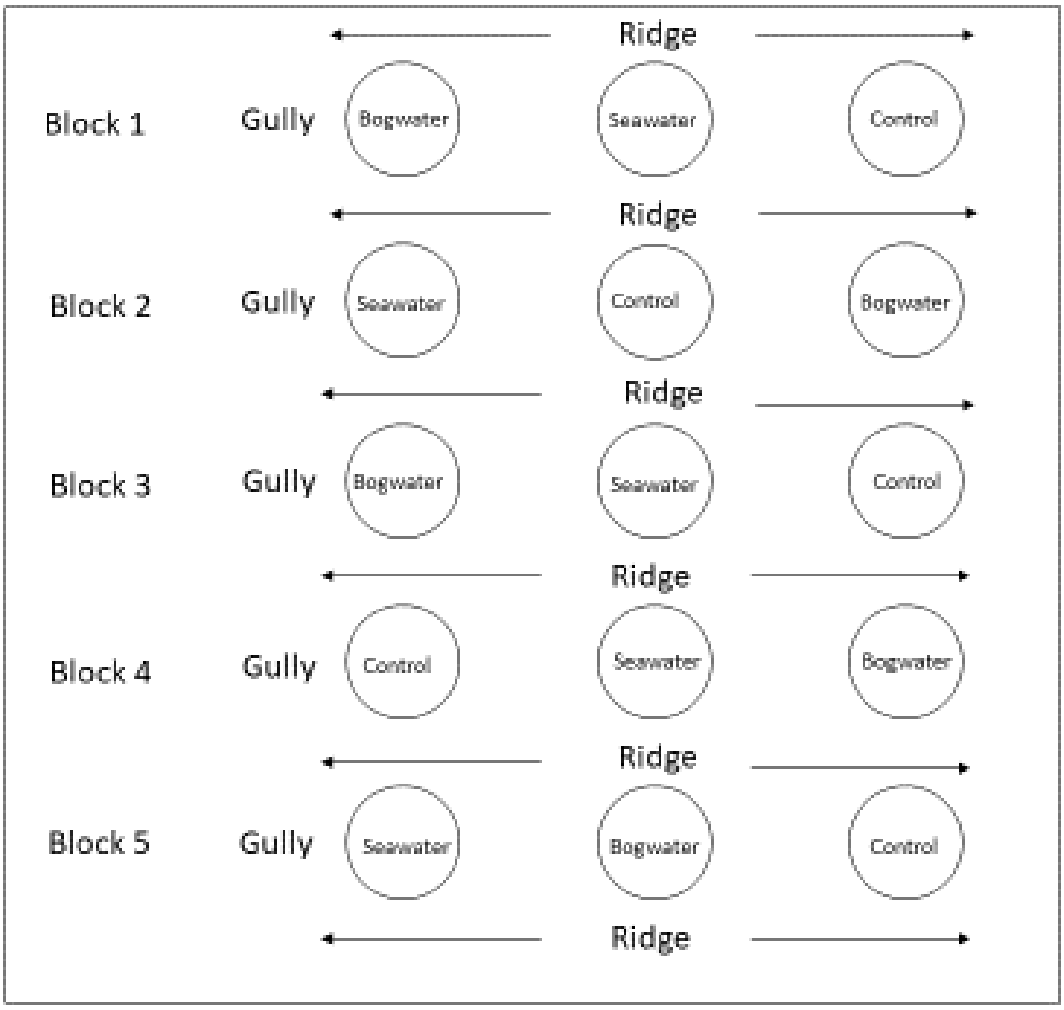
3.3.2 Experimental design

The experimental approach was to isolate plots of *Sphagnum*-dominated bog and apply sea water or control treatments *in-situ*. In February 2015, 15 plots were created to the north-east of the bog dome (Figs. 3.1, 3.2), in five blocks running east to west. This area of the peatland had formerly been the site of manual peat extraction and was last cut in the 1950's. The blocks were located within the former peat-cut areas that had re-vegetated over at least 65 years.

Within each block, three plots, approximately three meters apart, were created by inserting PVC tubing (length 1 m, diameter 315 mm) into the peat (table 3.1). This length was used in order to minimise lateral water movement between plots and the surrounding area. Plots were selected to have a similar vegetation composition (>90% *Sphagnum cuspidatum*, with some *Eriophorum angustifolium* present in all plots). Vegetation roots were sawn through to a depth of approximately 600 mm prior to inserting the tubes. Initially, the mean height of the collar rim to the internal plot vegetation surface (mean of four points) was 100 mm, whilst the external difference between vegetation surface and collar rims of the plots was between 80-90 mm, indicating that the insertion of the tubes caused slight compression in the column. However, after one month the distance to collar rim in the inner and outer vegetation were similar, and the internal edges of the plot were contiguous with the vegetation (i.e. there were no spaces between vegetation edge and tube). Within the plots, a one-metre long, 32 mm diameter tube with holes drilled at 100 mm interval (holes starting 100 mm below the vegetation surface) was inserted to a depth of 900 mm (with 100 mm protruding above the surface) for measurement of water table depth. Portable boardwalks were used around plots to minimise damage and reduce the possibility of ebullition caused by disturbance to the peat column during measurements.

The treatments commenced five weeks after the establishment of the plots to allow for settling of the collars and increases in rates of microbial respiration resulting from root damage. Three treatments were applied in each block: control (no water application), bog-water application (10 L of bogwater sourced from a nearby pool, hereafter BW) and seawater application (10 L of seawater from the adjacent coastline, hereafter seawater). The BW and seawater treatments were applied once on the same day (11th April 2015) within a four-hour window. Application of the treatments involved slowly pouring the water from a low height in order to minimise any physical damage (e.g. scouring) due to water impact.

Table 3.1 Schematic layout of plots within circled area in Fig 3.1 (not to scale).



3.3.3 Gas flux measurements

Monthly daytime measurements of CO_2 and CH_4 gaseous exchange in the light and dark were taken from April to August 2015, and repeated again in July 2016, using a portable greenhouse gas analyser (LGRNC, California; USA) attached to a hemispherical Perspex dome chamber (Sunlight plastics; Hampshire, UK) via tubing with a moisture filter on the inlet line. The base of the dome had a 40 mm diameter inflatable tube attached with silicone inflated to a low pressure to form a temporary seal around the rim of the collar. Within the chamber a solar irradiance meter and 9V fan were fitted, the latter for mixing air within the chamber.

Measurements of all plots were taken in a single day on each monthly visit between 1000-1600, so plots experienced similar weather and radiation conditions during sampling. During measurements, the water table tube was sealed to prevent direct water-atmosphere contact. CO_2 and CH_4 fluxes were measured both in sunlight and subsequently in the dark with an opaque cover. Simultaneously air temperature and light levels were recorded with a Campbell Scientific CR00r Delta T GP1 data logger (Campbell Scientific, Loughborough, UK; Delta T Devices, Cambridge, UK). Flux measurements lasted a minimum of 2.5 minutes at one second measurement frequency, with one minute for venting between measurements. Flux values were monitored in real-time allowing for identification of abnormal fluxes due to ebullition or leaks in the chamber seal, and subsequent re-measurement if required.

Fluxes were calculated by measuring changes in gas concentrations over a 120 second period selected from within measurement periods which lasted approximately 180 seconds in the field. Best-fit r^2 values were calculated for sequential sections and the most linear segment change in flux with an r^2 value ≥85% was included in analyses.

Fluxes with a maximum r^2 below 85%, or considered anomalous were assessed visually, with consideration of the conditions at the time of measurement, for inclusion or removal. Gap filling was required for 10.6% of CO_2 fluxes which did not meet these requirements (all CH_4 fluxes were ≥85% r^2), and was achieved by averaging replicate values by treatment.

CO_2 measurements in the light are termed Net Ecosystem Exchange (NEE) and include autotrophic and heterotrophic respiration as well as photosynthesis. Measurements in the dark are termed Ecosystem Respiration (ER) and include both autotrophic and heterotrophic respiration. ER values are always positive (efflux from the biosphere to the atmosphere), whilst NEE may be positive (efflux) or negative (net uptake by the biosphere from the atmosphere). Gross Primary Productivity (GPP), as the rate of CO_2 uptake by primary producers, was derived from the difference between NEE and ER, and must be negative, by rearranging the equation NEE=GPP+ER. The same technique was used for CH_4 fluxes, but only measurements taken in light conditions are shown here as there was no obvious or significant difference between light and dark CH_4 measurements and more data points were available for the light fluxes.

3.3.4 Environmental measurements

The potential for photosynthesis by representative species within each plot was measured monthly by the chlorophyll fluorescence technique (reported as *Fv/Fm*) using a Hansatech Photosynthesis Efficiency Analyser (Hansatech Ltd, King's Lynn, UK). Values range from 0-0.99, where a decrease in values indicating a reduction in the plants potential photosynthesis rates (Maxwell and Johnson 2000). Three dark adaptation clips were placed on the capitula of *S. cuspidatum* or the leaves of *E.angustifolium* for 10 minutes prior to measurement using a one second light pulse at 500 μmol m^{-2} s^{-1}.

Vegetation percentage cover was assessed in July of each year from 2015 to 2017 using a 5 cm^2 grid overlying each plot. Water table depth was measured prior to each gas flux measurement. Water samples were extracted from the dipwell via a tube and syringe and filtered using Dionex pre-filters (0.45 μm pore size) pre-flushed with 5 ml of sample water taken from the plot. Water samples were analysed in the laboratory for pH and conductivity using Mettler-Toledo FiveEasy FE20 and FE30 models respectively (Mettler-Toledo, Leicester, UK), and values are reported at 20°C.

3.3.5 Statistical analyses

A two-way mixed effects ANOVA was used with measurement date as the repeated measure and treatment (3 levels) as the fixed factor using SPSS v.22. Due to multiple failures to meet the assumptions of the statistical tests, data were rank transformed prior to analysis following the approach of Connover & Inam (1981). One-way ANOVA and Bonferroni adjusted Tukey post-hoc tests were used for simple and main effects analysis after any interactions between treatment and time were identified, with the α value set at ≤ 0.05. Results are presented as mean ±1 standard error.

3.4 Results

3.4.1 Environmental responses

Following application of the treatments, the water levels within both the seawater and bogwater (BW) plots rose and then took approximately one week to fall to levels similar to those of the control. Installation of the plots had no obvious visual effect (Fig. 3.2). There were no significant differences between plots in terms of light levels, soil temperature or water table depths at any gas measurement point (p>0.05; Appendix table 1). Prior to the treatments being applied, mean pH and conductivity values between plots assigned to the different treatments were all within one standard error ranging from 5.97 to 6.37 (pH) and 53 to 114 μS cm^{-1} (conductivity) (Fig. 3.3, Appendix tables 1 and 3). The addition of BW (pH 5.65, conductivity 0.01 mS cm^{-1}) had no significant effect on pH or conductivity (p>0.05) compared to control plots (p=0.58). The addition of seawater (pH 7.07, conductivity 49.4 mS cm^{-1}, salinity approximately 32 ppt) led to a significant decrease in plot pH ($F_{(2,12)}$=36.3, p<0.001) compared to both control and BW values between May and July 2015, (Fig. 3.3), but values for all treatments were similar in July 2016. Conductivity values were significantly higher overall in the seawater plots following treatment than both control and BW plots on all measurement dates from May 15 onwards ($F_{(5.6, 33.7)}$=5.75, p<0.001) and were significantly higher in seawater than either control or bogwater from May-15 onwards (Appendix table 5).

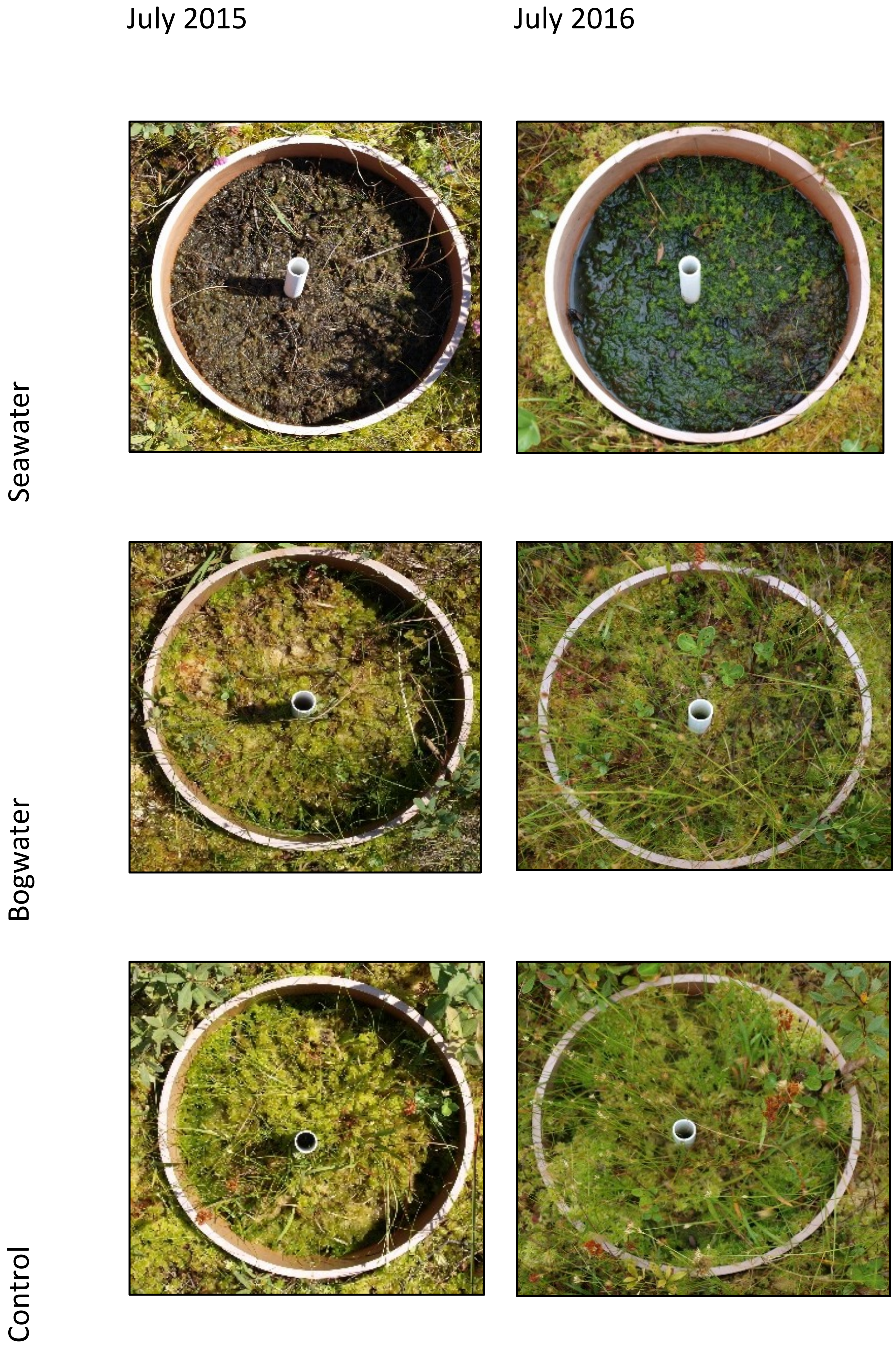


Fig. 3.2. Plots from post treatment July 2015 and 2016 after a single treatment in April 2015. Within each treatment, the same plot has been used across the time period for the photograph. Note the rise of the internal vegetation surface within the control and bogwater plots compared to seawater.

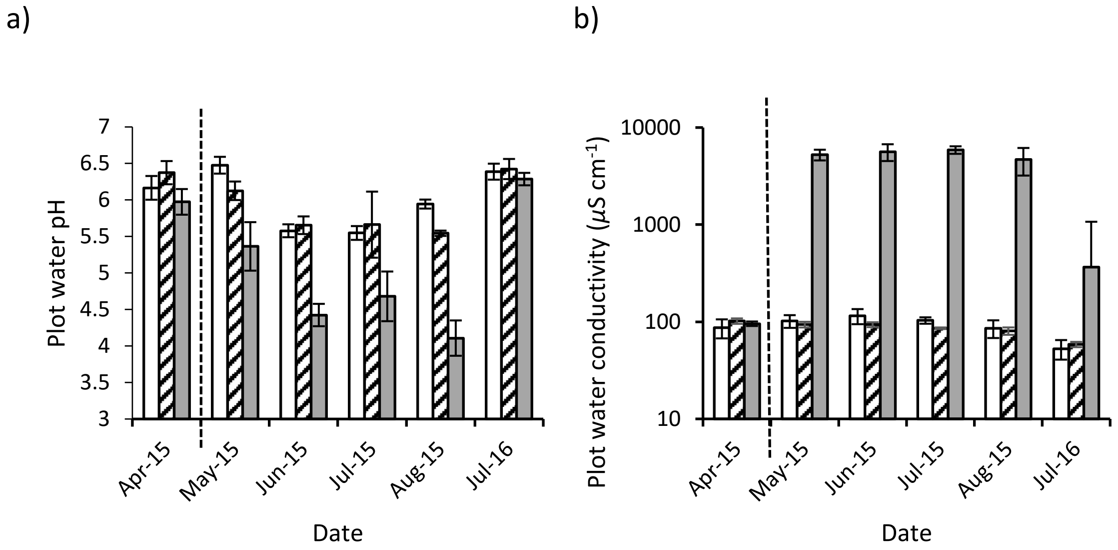


Fig. 3.3. Mean monthly pH (a) and conductivity (b) values of water taken from water table depth tubes within experimental plots. Note the conductivity Y axis is a logarithmic scale. Values to the right of the dashed line are post treatment. Control are blank, bogwater are striped, and seawater are grey. Error bars represent one standard error.

3.4.2 Vegetation responses

Prior to the application of treatments, the plots were similar in their visual appearances, dominated by *Sphagnum cuspidatum*. Mean percentage cover of mosses between 2015-2017 in control and BW plots ranged from 95-100% (Fig. 3.2 Fig. 3.4). Mean vascular cover in control plots ranged from 16-25% in control plots, and 15-38% in BW. In the seawater plots, the treatment led to a flattening of the vegetation surface, blackening of *Eriophorum angustifolium* and *Rhynchospora alba* stems, and discoloration of *Sphagnum* species into a dark brown colour. Seawater treated *Sphagnum* plants were also noted to fragment upon contact. *Sphagnum* moss cover in seawater plots post-treatment was 52% in 2015, the remainder was decomposed. However, by 2017 green *Sphagnum* moss cover had risen to 81% in these plots, whilst vascular cover changed little, ranging from 13% to 15%.

The discolouration of *Sphagnum* in the seawater plots (Fig. 3.2) was not reflected in chlorophyll fluorescence values which showed little variation in season or between treatments. Any slight differences in treatment were not statistically significantly with *Fv/Fm* values ranging from 0.38 to 0.53 (Appendix, table 2). Chlorophyll fluorescence measurements on the blackened foliage of *E. angustifolium* produced errors in the readout so measurements were taken from green foliage when possible. However, measurements of the tips of leaves that were not damaged, or on the basal parts of foliage that grew after the water level had fallen below the surface did not show any statistically significant differences between seawater and the other treatments ($p>0.05$) with values ranging from 0.35 to 0.74 (Appendix, table 2).

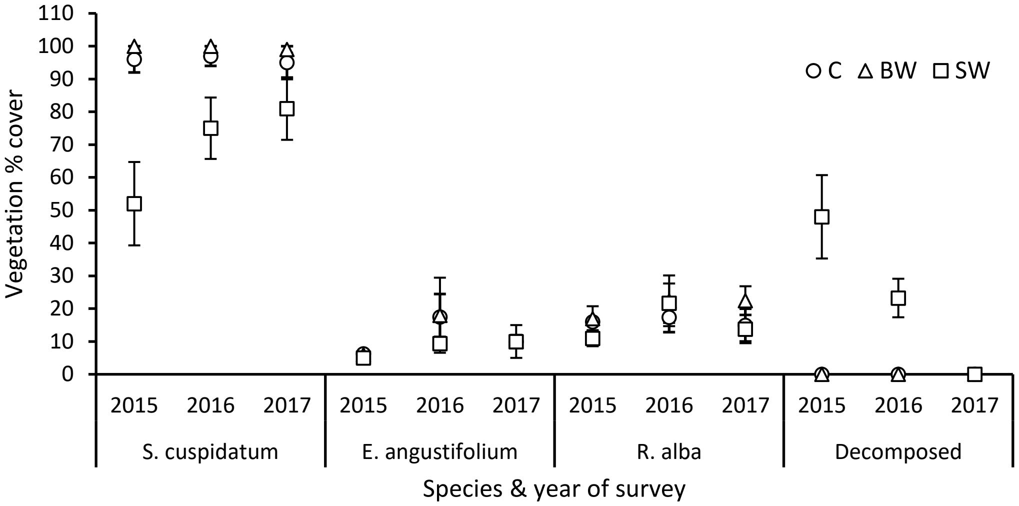


Fig. 3.4. Mean vegetation percentage cover of plots by treatment in July 2015-2017. The single treatment, seawater (SW), bogwater (BW), or control (C) took place in April 2015. Error bars represent one standard error.

3.4.3 Gas flux responses

There was a significant overall effect of the seawater treatment on CH_4 fluxes ($F_{(2,12)}$=9.35, p=0.004) with fluxes significantly lower than control from May to July 2015, and significantly lower than bog water from May to August 2015 (Fig 3.5a). Calculated as a percentage of the control values, the lowest inhibitive effect of the seawater treatment was 60% in April 2015, and highest in July 2016 at 102%. In all other months, CH_4 fluxes were inhibited by more than 80% by the seawater treatment relative to control. In April 2015, there was a negative flux of CH_4 from the atmosphere to the bog of -0.0002 μmol CH_4 m^{-2} h^{-1} in the seawater treatment, indicating the uptake of CH_4.

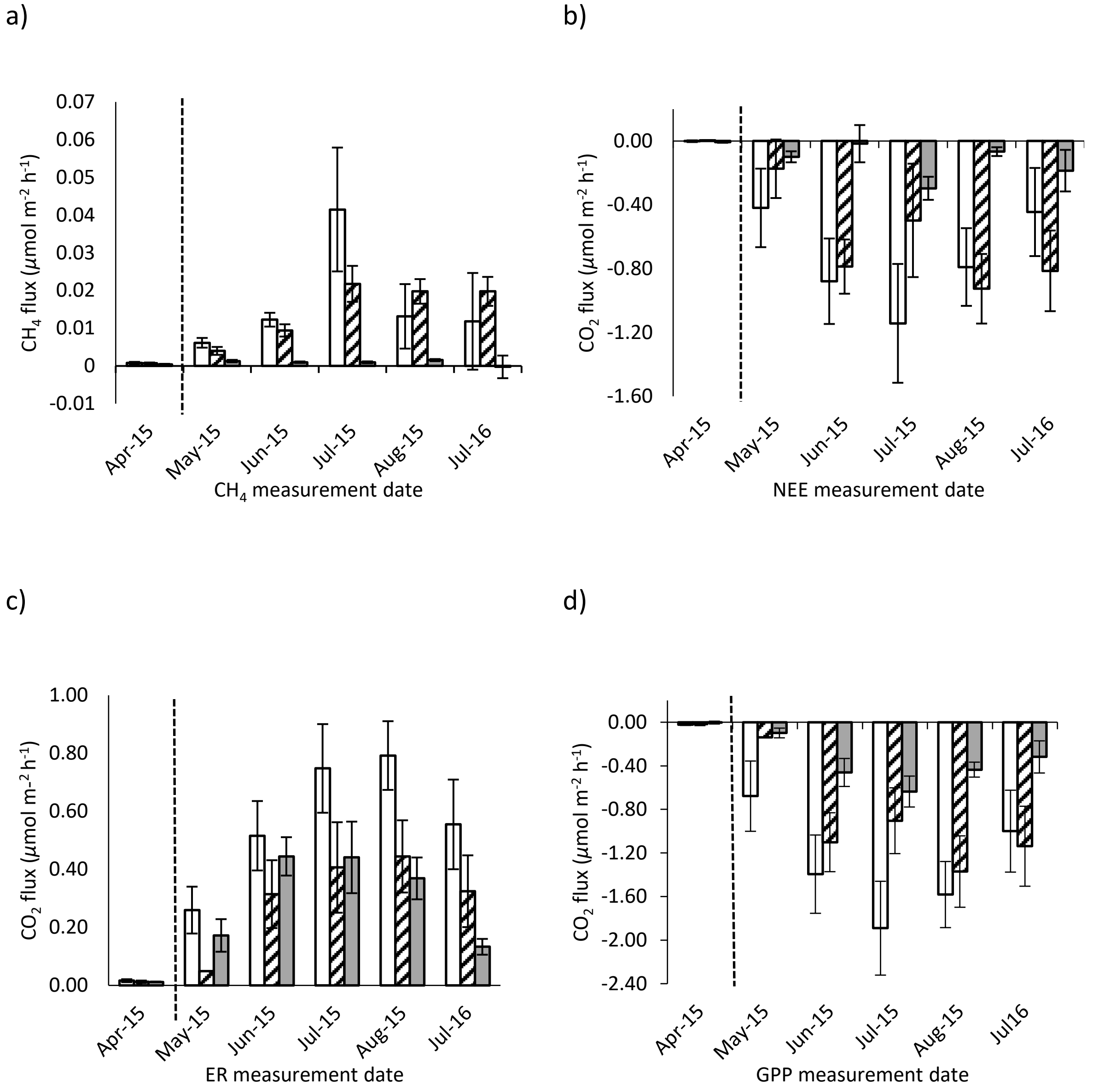


Fig. 3.5. Mean fluxes of (a) CH_4; (b) Net ecosystem exchange; (c) Ecosystem respiration; (d) Gross primary productivity. Values to the right of the dashed line are post treatment. Control are blank, bogwater are striped, and seawater are grey. Error bars represent one standard error.

Net ecosystem exchange (Fig. 3.5b) showed strong seasonal variation in the control plots from almost zero in April 2015 to around -1.1 μmol m^{-2} s^{-1} in August (Appendix table 4). NEE rates were lowest in seawater plots throughout 2015 and in July 2016. Inhibition of NEE in seawater plots relative to control ranged from 0 in April 2015 to 98% in June 2015 but was not statistically significant (Appendix table 5).

Ecosystem respiration (Fig. 3.5c) was higher in the control plots than both seawater and BW in May to July 2015. There was a trend of increasing ER from spring to summer in 2015 regardless of treatment. Mean ER was highest in July 2015 and lowest in April 2015 for both the control and BW treatments, whilst the highest seawater values were in June 2015 and the lowest in April 2015. Mean percentage inhibition of ER in seawater plots relative to control ranged from 25% in April 2015 to of 46% in July 2015. There were statistically significant differences between treatments in August 2015 ($F_{(2,12)}$,12.2, p=.001) with seawater ER rates lower than both control (p=.001) and bog water (p=.029), as well as a significant interaction between time and treatment ($F_{(5,31)}$=2.69, p=.038) (Appendix table 5). Due to missing values, the statistical significance for May 2015 was not calculated.

The derived gross primary productivity rates showed the same seasonal pattern of change as NEE and ER (Fig. 3.5d). Mean GPP values were greatest in control treatments, reaching -1.891 μmol CO$_2$ m^{-2} h^{-1} in July 2015, whist the maximum mean value for seawater treatments was -0.636 μmol CO$_2$ m^{-2} h^{-1} in the same period. July 2016 was the highest mean value in BW treatments at -1.138 μmol CO$_2$ m^{-2} h^{-1}. GPP inhibition in seawater relative to control was >65% at all measurement points, and greatest in May 2015 at 85%. A significant main effect of treatment was identified with both bog water and control values greater than seawater collapsed across time (*p*=0.04; *p*=.001; Appendix table 5).

3.5 Discussion

A one off flood caused major increase in conductivity and a drop in pH. This resulted in a short-term effect on *Sphagnum* growth and almost complete inhibition of CH_4 emissions along with large reductions in photosynthesis and respiration which suggests the vulnerability of coastal bogs to sea level rise and storm surges.

The decrease in pH has also been reported in *Sphagnum* peatlands subjected to seawater flooding. pH decreased with both increases in salinity (Montemayor et al, 2008), or electrical conductivity (Montemayor et al, 2015). In these studies, the change in pH was associated with *Sphagnum's* high cation exchange capacity, when hydrogen ions are released by Sphagna, acidifying into the surrounding waters, (Clymo, 1964). Pugh et al (1996) found pH values fell with increasing calcium ion concentration in *Sphagnum* bog peat contaminated with road salt runoff, with hydrogen ions being displaced from the peat as sodium, calcium and magnesium competed with hydrogen ions for exchange sites on the peat surface. These studies were undertaken on peat without the vegetation component, however, it is likely that the same process occurred within this study, or may even have been accentuated by the presence of damaged or dead *Sphagnum* plants that can lower the pH of surrounding waters (Clymo, 1964).

It was hypothesised that methane fluxes to the atmosphere would decrease relative to control values, and the findings in this study are consistent with previous studies in freshwater marshes and peat soils, where salinity inputs reduced CH_4 emissions to the atmosphere. (Chambers 2014; Neubauer 2013; Wang 2017; Weston 2006). The analysis of short-term potential methane emissions in experiments in freshwater soils have shown inhibition of CH_4 up to 94% (Chambers et all, 2011) similar in scale to the findings in this study. However, inhibition in this study continued for 15 months following treatment contrasted with Chambers et al (2011) short term three-week laboratory experiment, although no data were available for the winter months.

The presence of sulphate in seawater has been shown to be a strong determinant of CH_4 responses to seawater, as sulphate reduction has a greater energy yield than and is thermodynamically preferred to methanogenesis (Capone and Kiene, 1988; Chambers 2014; Dise and Verry 2001). Weston et al (2006) found that when freshwater marsh soils in which methanogenesis accounted for over 60% of organic matter mineralisation were treated with seawater, this microbial process was replaced by sulphate reduction that accounted for 95% of organic matter mineralisation after 12 days at 9.9 ppt.

The ecosystem respiration (ER) responses in this study are in keeping with those reported in the literature for peat soils treated with seawater for four months (Brouns et al, 2014) and freshwater marsh soils treated with seawater for 3.5 years (Neubauer et al, 2013). However, both these studies used brackish seawater at salinities of less than 4 ppt compared to 32 ppt in this study, and measured only soil ER responses. At higher seawater concentrations, Chambers et al (2014) and Weston et al (2011) found ER flux rates to increase at concentrations of 35 ppt and 14 ppt over three weeks and one year respectively. Furthermore, with the exception of Brouns et al (2014), the other studies were conducted on tidal freshwater marsh soils derived from vegetation and possibly microbial communities distinct from those found in ombrotrophic peatlands.

The rates of photosynthesis expressed as NEE and GPP were lower in the sea water than control treatments, but statistically significant differences were not seen in NEE due to the large inter-plot variation, though the rates of GPP were significantly reduced by the seawater treatment. Inhibition of photosynthesis is a common response to salinity in most moss studies, photosynthetic uptake declines when exposed to seawater or salinity, often resulting in reduced biomass production and plant death. (Bates 1976; Bates and Brown 1975; Bates et al 2009; Pouliot 2013; Wilcox 1984).

The apparent lack of effect of seawater on chlorophyll fluorescence responses in *Sphagnum* may indicate that the light harvesting photosystem-2 mechanisms that the method assesses may not have been impaired by the treatments, or that the frequency of measurement missed the effects. Maricle et al (2007) found estuarine halophytic grass chlorophyll fluorescence values in four species were unaffected by seawater treatments of 30 ppt, despite reductions in net photosynthesis of up to 75%.

Although vegetation communities in freshwater or oligohaline habitats have demonstrated recovery from short term seawater pulses (Flynn et al, 1995; Howard and Mendelssohn, 2000), and some tolerance to low concentrations of seawater has also been noted in bryophytes (Bates & Brown, 1975; Callaghan and Farr, 2018), *Sphagnum sp.* have shown little tolerance to salinity exposure, even at low concentrations of NaCl (Wilcox, 1984; Wilcox & Andrus, 1987). Halophytic vascular species possess tolerance mechanisms which may ameliorate the effects of salinity (Munns & Tester, 2008) and allow them to increase a foothold in ombrotrophic peatlands in the event of suppression of *Sphagnum* dominance. Regeneration or replacement of marsh vegetation has been reported following seawater flooding in marshes (Flynn et al., 1995; McKee & Mendelssohn, 1995). In cutover peatlands following seawater flooding, Montemayor et al (2015) found sods of *Juncus balticus* were less successful in terms of flowers per stem, stems per sod and percentage survival five years after a seawater flood event. However, survival of other species such as *Spartina pectinata* was unaffected, suggesting that a zonation of species may develop across a saline affected peatland. Maricle et al (2007) identified differential responses in net photosynthetic uptake and respiration between three halophytic C_4 grass species. This may be more likely if gradients across the site lead to unequal distribution of marine salts and differences in drainage or retention times (Montemayor et al, 2008).

Although no major shift from *Sphagnum* to vascular domination was found in this experiment, it is likely that repeated and sustained flooding would likely lead to the development of a clearer gradient of saltmarsh to bog gradient (i.e. halophytic to ombrophytic vegetation community). Such a transition would likely be found in a maritime bog such as Cors Fochno, for example, Whittle and Gallego-Sala (2016) identified a Scottish coastal bog where the saltmarsh-ombrotrophic bog gradient extended inland 2 km from the coast. The gradient was expressed not only phytosociological, but also along chemistry (pH, conductivity) and carbon accumulation rates. Alternatively, repeated and sustained marine ingressions of peatlands initially formed under freshwater conditions has led to the development of saltmarshes overlying ombrotrophically formed peat along the western Atlantic coast of Ireland, which Cott et al (2012) characterised as ‘fringe marshes’. If seawater-flooding events are repeated over a relatively short timescale, this may result in permanent damage to the dominant vegetation, resulting in a shift from ombrotrophic to halophytic vegetation communities, an increase in deposits carried onto the peatland by the seawater, and eventual transformation into a saline ecosystem, though the initial oligotrophically derived deeper peats may be preserved.

In a harvested bog inundated by seawater during a storm surge (Mouniemme and Price, 2007) identified downward movement of salts through the peat column, and were identified at 95cm depth two years after the storm surge, although this was at a salinity of 3-4 ppt, values in the top 22cm were between 2-10ppt-probably beyond tolerance of many species. Raised features (e.g. access road) limited the spread of the storm surge across the site (Mouniemme & Price, 2007). Seawater from surge drained into low lying areas and drainage channels. Subsequent pumping attempts within the same year found seawater contamination of peat

A consideration for peatland managers is that given the NEE values remained negative following the treatment, and no evidence of major shifts in vegetation community were observed, there may be conditions where a managed saline flood could be of benefit in terms of the peatland's carbon balance. For example, during extreme temperatures, drought or water stress, peatlands may become CO_2 sources to the atmosphere due to reduced GPP and increased ER (Bragazza et al 2016; Dorrepaal et al, 2009, Helfter et al 2015), both of which were reduced in this experiment. A further benefit would be the suppression of CH_4 emission, particularly when considering methane's greater global warming potential. However, consideration should be given to whether repeated flooding events (managed or natural) might result in vegetation changes, and as to whether the storage and sequestration of carbon or the preservation of an intact ecosystem has greater priority. Considering that tidal salt marshes also accumulate carbon in their soils (Chastain et al, 2018; Drake et al 2015), and that even brackish water (5-30ppt) can inhibit methane emissions (Poffenbarger et al, 2011), and that low-lying estuarine peatlands are likely to experience seawater flooding due to climate change (Nicholls, 2004; Wong 2014), a change in focus from preservation of an ecosystem type towards carbon management may be a more economic and practical management pathway.

3.6 Conclusions

In the first known reported results of a one off seawater flooding event on an ombrotrophic peatland, CO_2 exchange fluxes and CH_4 gas emissions to the atmosphere were reduced, and vegetation appeared damaged, though recovery was evident one year following from the inundation. The eventual trajectory of low lying peatlands at risk of coastal flooding is likely to be development into a salt-marsh halophyte dominant vegetation community overlying *Sphagnum* peat deposits.

3.7 Appendices

Table 1. Chemistry of treatment waters taken from semi-permanent bog pool (BW) close to the experimental site and Irish Sea coastline (seawater) in April 2015. Conductivity readings were taken at 20°C.

	K	Salinity				Ions (mg/l)						
Source	(*m*S/cm)	ppt	pH	Na^+	Cl^-	SO_4^{2-}	Mg^{2+}	Ca^{2+}	K^+	NO_3^{1-}	PO_4^{3-}	NH_4+
SW	49.4	32.3	7.07	6689	11328	1803	743	391	356	247	0	0
BW	0.01	0.01	5.65	13.02	20.63	1.15	1.57	1.50	0.62	0.15	0.3	0.04

Table 2. Mean monthly values (±1se) for *Fv/Fm*. The value for *E. angustifolium* in July 16 was from one value only.

	Date	Control	BW	seawater
S. cuspidatum	Apr15	0.39 ± 0.06	0.38 ± 0.04	0.42 ± 0.08
	May15	0.54 ± 0.06	0.42 ± 0.06	0.51 ± 0.05
	Jun15	0.48 ± 0.03	0.44 ± 0.06	0.44 ± 0.08
	Jul 15	0.52 ± 0.05	0.50 ± 0.05	0.43 ± 0.06
	Aug 15	0.47 ± 0.05	0.50 ± 0.08	0.53 ± 0.01
	Jul 16	0.23 ± 0.05	0.29 ± 0.1	0.40 ± 0.05
E. angustifolium	Apr15	0.47 ± .08	0.51 ± .06	0.53 ± .07
	May15	0.45 ± .05	0.61 ± .07	0.51 ± .13
	Jun15	0.57 ± .03	0.66 ± .08	0.52 ± .10
	Jul 15	0.68 ± .02	0.71 ± .08	0.35 ± .05
	Aug 15	0.74 ± .03	0.71 ± .01	0.60 ± .07
	Jul 16	0.48 ± .09	0.56 ± .07	0.67

Table 3. Mean monthly values (±1se) for conductivity (at 20°C), pH and water table depth (WTD-depth from surface to water table).

	Date	Control	BW	seawater
Conductivity (μS cm^{-1})	Apr 15	86.7 ± 19.22	101.8 ±6.58	95.6 ±5.11
	May 15	101.7±7.81	93.6 ±1.61	5248 ±523.40
	Jun 15	114.7 ±17.74	93.5 ±7.04	5623 ±1479.13
	Jul 15	103.3 ±12.03	85.8 ±3.62	5884 ±707.20
	Aug15	85.8 ±12.0	80.4 ±3.96	4682 ±739.94
	Jul 16	52.8 ±4.92	58.4 ±6.15	364.2 ±179.35
pH	Apr 15	6.17 ±0.162	6.37 ±0.159	5.97 ±0.176
	May 15	6.48 ±0.095	6.13±0.452	5.36 ±0.340
	Jun 15	5.58 ±0.062	5.65 ±0.036	4.42 ±0.242
	Jul 15	5.55 ±0.110	5.66 ±0.138	4.68 ±0.085
	Aug15	5.94 ±0.120	5.54 ±0.378	4.11 ±0.061
	Jul 16	6.39 ±0.174	6.42 ±0.159	6.29 ±0.294
WTD	Apr 15	-9.9± 0.185	-9.88± 0.245	-9.5± 0.418
	May 15	-10.3± 0.678	-11.1± 0.374	-9.9± 0.765
	Jun 15	-13.2± 0.557	-14.1± 1.366	-13.1± 0.534
	Jul 15	-11.8± 0.539	-13.3± 0.583	-12.6± 0.485
	Aug15	-10.3± 0.930	-10.7± 1.586	-10.4± 0.485
	Jul 16	-7.4± 1.077	-5.8± 1.530	-4.75± 0.678

Table 4. Gas flux monthly means (±1se) for CH_4, net ecosystem exchange, ecosystem respiration and gross primary productivity. May 2015 GPP and ER values were gap filled from single values and so margins of error are not appropriate.

	Date	Control	BW	seawater
CH_4	Apr 15	0.001± 0.0002	0.001± 0.0002	0.0004± 0.0003
	May 15	0.006± 0.0013	0.004± 0.0010	0.001± 0.0003
	Jun 15	0.012± 0.0018	0.009± 0.0016	0.001± 0.0002
	Jul 15	0.041± 0.0164	0.022± 0.0048	0.001± 0.0002
	Aug 15	0.013± 0.0090	0.020± 0.0033	0.002± 0.0003
	Jul 16	0.012± 0.0129	0.020± 0.0038	-0.0002± 0.003
NEE	Apr 15	-0.005± 0.0045	0.009± 0.0092	-0.005± 0.0129
	May 15	-0.419± 0.2462	-0.174± 0.1835	-0.099± 0.0346
	Jun 15	-0.879± 0.268	-0.787± 0.1699	-0.017± 0.1167
	Jul 15	-1.143± 0.3723	-0.497± 0.3555	-0.296± 0.0723
	Aug 15	-0.790± 0.2435	-0.926± 0.2181	-0.066± 0.0276
	Jul 16	-0.445± 0.2763	-0.814± 0.2528	-0.186± 0.1302
ER	Apr 15	0.016± 0.0051	0.012± 0.0044	0.012± 0.0012
	May 15	0.260± 0.0808	0.049± NA	0.172± 0.0562
	Jun 15	0.516± 0.1196	0.315± 0.117	0.445± 0.0661
	Jul 15	0.748± 0.1528	0.407± 0.1559	0.340± 0.0704
	Aug 15	0.792± 0.1184	0.445± 0.1244	0.369± 0.0721
	Jul 16	0.555± 0.1545	0.325± 0.1237	0.133± 0.0272
GPP	Apr 15	-0.022± 0.0078	-0.018± 0.0133	-0.003± 0.0130
	May 15	-0.679± 0.3225	-0.138± NA	-0.099± 0.0446
	Jun 15	-1.395± 0.3593	-1.101± 0.2703	-0.461± 0.1284
	Jul 15	-1.891± 0.4306	-0.904± 0.3019	-0.636± 0.1419
	Aug 15	-1.582± 0.3033	-1.371± 0.3276	-0.435± 0.0686
	Jul 16	-1.000± 0.3758	-1.138± 0.3668	-0.319± 0.1475

Table 5. One-way ANOVA (main or simple main effects) and post hoc Bonferroni adjusted Tukey tests for gas fluxes, pH and conductivity measurements. Replicates for pH were not available for statistical analyses in July 16. Significant results are highlighted in bold.

		ANOVA	C Vs BW	C Vs SW	BW Vs SW
CH_4	Apr 15	$F_{(2,12)}$.593, p=.568	NA	NA	NA
	May 15	$F_{(2,12)}$,10,1 p=.003	.375	**.002**	**.028**
	Jun 15	$F_{(2,12)}$,14.8, p=.001	.399	**.001**	**.005**
	Jul 15	$F_{(2,12)}$,13.2, p=.001	.699	**.001**	**.005**
	Aug 15	$F_{(2,12)}$,4.9, p=.027	.764	.095	**.027**
	Jul 16	$F_{(2,12)}$,3.5, p=.063	NA	NA	NA
ER	Apr 15	$F_{(2,12)}$.325, p=.728	NA	NA	NA
	May 15	$F_{(2,12)}$,14.8, p=..233	NA	NA	NA
	Jul 15	$F_{(2,12)}$3.21, p=..076	NA	NA	NA
	Jul 15	$F_{(2,12)}$,4.5, p=.035	.057	.057	1.0
	Aug 15	$F_{(2,12)}$,12.2, p=.001	.169	**.001**	**.029**
	Jul 16	$F_{(2,12)}$.325, p=.728	NA	NA	NA
pH	Apr 15	$F_{(2,12)}$2.04, p=1.73	NA	NA	NA
	May 15	$F_{(2,12)}$13.5, p=.001	.622	**.001**	**.005**
	Jun15	$F_{(2,12)}$13.2, p=.001	.699	**.001**	**.005**
	Jul15	$F_{(2,12)}$13.3, p=.001	.697	**.005**	**.001**
	Aug15	$F_{(2,12)}$.045, p=.956	NA	NA	NA
Conductivity	Apr 15	$F_{(2,12)}$1.6, p=.243	NA	NA	NA
	May 15	$F_{(2,12)}$13.2, p=.001	.699	**.005**	**.001**
	Jun15	$F_{(2,12)}$12.3, p=.001	.937	**.004**	**.002**
	Jul15	$F_{(2,12)}$13.2, p=.002	.699	**.005**	**.001**
	Aug15	$F_{(2,12)}$12.2, p=.001	.993	**.003**	**.003**
	Jul16	$F_{(2,12)}$ 13.9, p=.001	.548	**.001**	**.005**

Chapter 4

Peatland responses to warming and drought

4.1 Abstract

Predicted changes in the global climate, including mean annual surface temperature and precipitation regimes are expected to have impacts upon semi-natural ecosystems, which may have important consequences for important regulating ecosystem services including the exchange of carbon dioxide between atmospheric and terrestrial pools.

During a four-week artificial drought imposed on an ombrotrophic peatland undergoing long term temperature manipulation, we measured gaseous CO_2 fluxes in a 3x4 factorial field manipulation experiment on a maritime ombrotrophic peatland on the west cost of Wales, UK. Treatments involved passive warming using open topped chambers, simulated summer droughts enforced by reducing the water table by pumping water from the plots, and a combination of the two treatments, as well as control plots.

Following the onset of water table drawdown, Ecosystem Respiration (ER) flux rates from the peatland to the atmosphere initially increased sharply in the combined warm and drought treatment. Mean Net Ecosystem Exchange (NEE) flux rates for the drought period were significantly higher than all other treatments, indicating the fluxes from the combined warm and drought plots were sources of CO_2 from the peatland to the atmosphere during the drought.

The results of this study indicate that in a future scenario of raised mean summer air temperatures, a short term drought in a warmer summer will lead to a shift in the role of ombrotrophic peatlands being sinks of atmospheric $CO_{2,}$ to becoming sources whilst water availability in the peat column is low.

4.2 Introduction

Gaseous carbon dioxide (CO_2) fluxes in ombrotrophic peatlands are closely associated with hydrology and temperature, the overall effect of which results in the peatland being a carbon source, or a carbon sink (Helfter et al 2015). These ecosystems can sequester and store atmospheric sources of carbon over millennia and this has led to the accumulation of an estimated 500 Gt of carbon in peatland soils, the majority of which are in the northern hemisphere, between 50 and 70° north (Moore, 2002; Yu 2012). Therefore, they warrant detailed investigations into how they will react to predicted changes in future climate scenarios. Observations and predictions of global climate change indicate that an increase in global mean temperature, and increase in the frequency and severity of droughts is increasing and likely to do so in the future (Stocker et al 2013).

Increases in mean annual air temperature of approximately 1°C over the long term are believed to have led to increases in the rates of carbon sequestration in northern peatlands based on paleo-ecological records, and are predicted to do so in the future with increasing temperatures (Charman et al 2013). This is primarily due to an increase in primary productivity, particularly by *Sphagnum* species, which can increase their photosynthesis rates in conditions of increased temperatures (Haraguchi et al 2011; Robroek et al 2007).

Other studies argue that an estimated 38-100 Mt C y^{-1} may be released to the atmosphere from northern peatlands if near term (decadal) temperatures rise by 1°C (Dorrepaal et al 2009). In both fens and bogs, increases in temperature may result in increases in both ecosystem respiration and primary productivity, which may depend on antecedent conditions affecting *Sphagnum* growth, particularly early in the growing season. However, the majority of studies conclude CO_2 uptake is likely to exceed respiration losses to the atmosphere. (Bell et al 2018; Chivers et al 2009; Dorrepaal et al 2009; Kim et al 2012; Lindroth et al 2007; Oechel et al 1998), providing water availability remains adequate.

An increase in the depth of the water table can increase ecosystem respiration rates (more strongly from subsurface peat than plant respiration) and can result in slight changes or strong reductions in the overall net ecosystem exchange, leading a peatland becoming a weaker CO_2 sink or slight source to the atmosphere (Ballantyne et al 2014; Chivers et al 2009; Helfter et al 2015; Riutta et al 2007). Desiccation of *Sphagnum* species results in reduced CO_2 uptake and increased autotrophic respiration (Bubier et al 2003), and may result in long term plant damage (Bragazza 2008) and vegetation community change (Heijmans et al 2008).

Whether the effect of temperature increase or depth to water table has the strongest effect on the CO_2 balance when co-occurring is unclear. An increase in temperature combined with a decrease in desiccation results in a decline in the rate of carbon accumulated in peatlands, but the carbon sink function is still retained (Bragazza et al 2016). Whilst Lafleur et al (2005) found temperature to be the strongest determinant of ecosystem respiration in a *Sphagnum*-shrub ombrotrophic bog, Pearson et al (2015) conversely found depth to water table to have a stronger effect on NEE on a boreal sedge fen. In a temperature and hydrology manipulation experiment, Updegraff (2001) found soil temperature to be the strongest determinant of ecosystem respiration, with no effect of water table depth or vegetation community, but the effect of drought may be additive if it occurs during periods of increased temperatures (Bragazza et al 2016; Helfter et al 2015).

The aim of this study was to quantify the effect of four years of mean annual temperature increase and artificial droughts on the summer CO_2 fluxes of an ombrotrophic peatland experiencing drought conditions. We tested the hypothesis that a combined medium term increase in air temperature and short-term repeated increase in depth to the water table would result in; 1) increased ecosystem respiration rates, 2) decreased gross primary productivity rates, resulting in 3) a decrease in net ecosystem exchange rates compared to control.

4.3 Methods

4.3.1 Experimental design

The approach was to experimentally isolate plots of *Sphagnum*-dominated bog and apply continuous warming and seasonal summer drought manipulation treatments in-situ. Our study was conducted in summer of 2014 after four years of combinations of long-term warming and following two previous simulations of drought in drought and warmed-drought plots (2010 and 2011) as part of the EU-Biodiversa funded 'Peatbog' project. In 2010, twelve 4 m^2 plots in three blocks were established on Cors Fochno, a lowland raised bog covering 6.5 km^2, of which 4 km^2 is active raised bog, in west Wales (Ordnance Survey grid reference: SN 636 926).

Plot walls were formed of conjoined non-permeable plastic piling sheets and were assigned one of four treatments; drought, warmed-drought, warmed and control. The control and warmed plots had 0.5m depth piling with holes drilled along their lengths to mimic the disturbance involved in the installation of deeper pilling but allow for subsurface water movement between the plots and the surrounding bog. The drought and warmed-drought plots had 1.5m depth undrilled piling, intended to minimise recharge of the peat column after pumping with water from the surrounding system (Figs 4.1 & 4.2).

The warm and warmed-drought plots also had an octagonal open topped chamber (OTC) constructed of 2.5mm Perspex (Arft et al 2010; Marion et al 1997), which have been shown to passively increase air temperatures within plots by approximately 1-2°C (Chivers et al 2009; Marion et al., 1997; Ward et al 2013).

In addition, the drought plots had 1 m length, 110mm diameter tubes inserted flush with the *Sphagnum* surface for lowering the water table (see below), and the peat within them excavated so they remained hollow. Each plot had two 110 mm diameter 200 mm length tubes inserted with 50 mm proud of the surface for CO_2 flux measurements.

Our study was conducted in the summer of 2014 after four years of long-term warming of warmed and warmed-drought plots and following two previous simulations of summer drought in drought and warmed-drought plots over six weeks in 2010 and 2011. Long-term changes in the experiment will be discussed elsewhere; here our focus is on short-term responses to drought using a high-frequency measurement series. We specifically aim to test whether four years of warming has modified carbon cycle responses to drought relative to plots which have not experienced this warming.

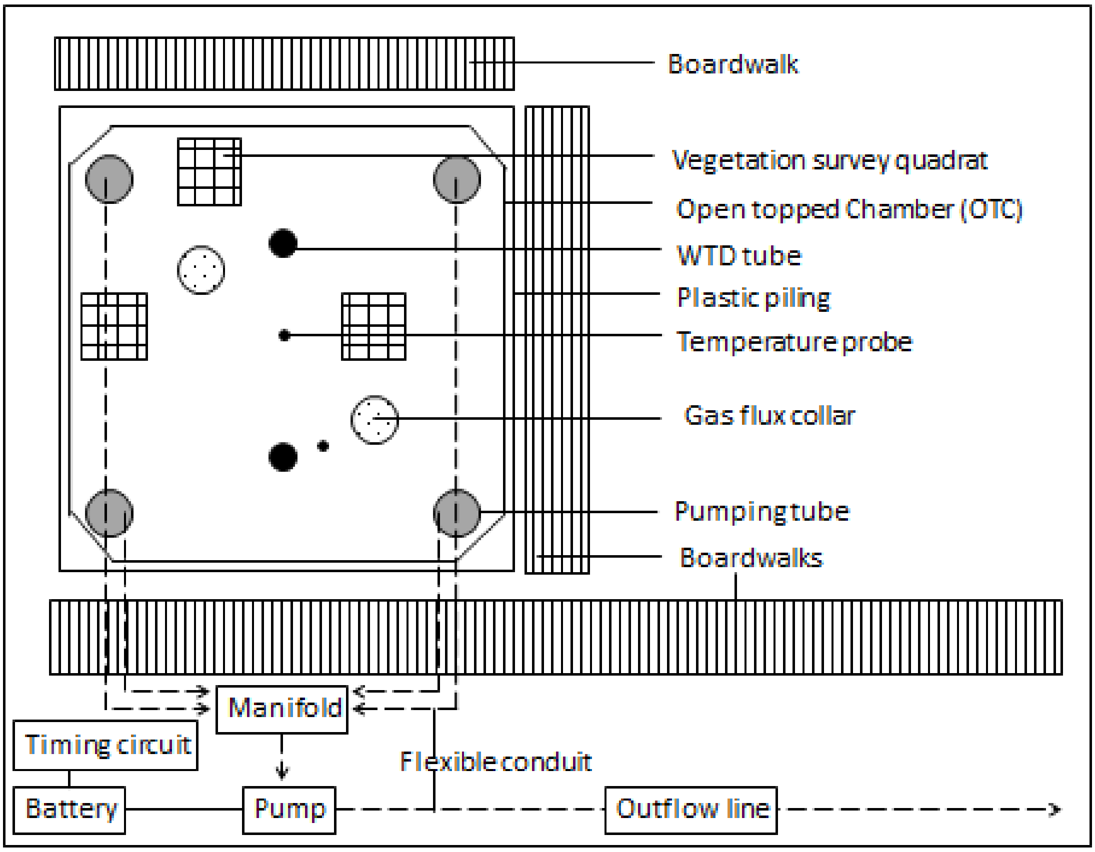


Fig. 4.1. Schematic overview of combined Drought and Warmed treatment including water table depth (WTD) measurement tubes. Warm only plots lacked the pumping tubes and associated pump equipment. Drought only plots lacked the OTCs. Control plots had neither pumping equipment nor OTCs.

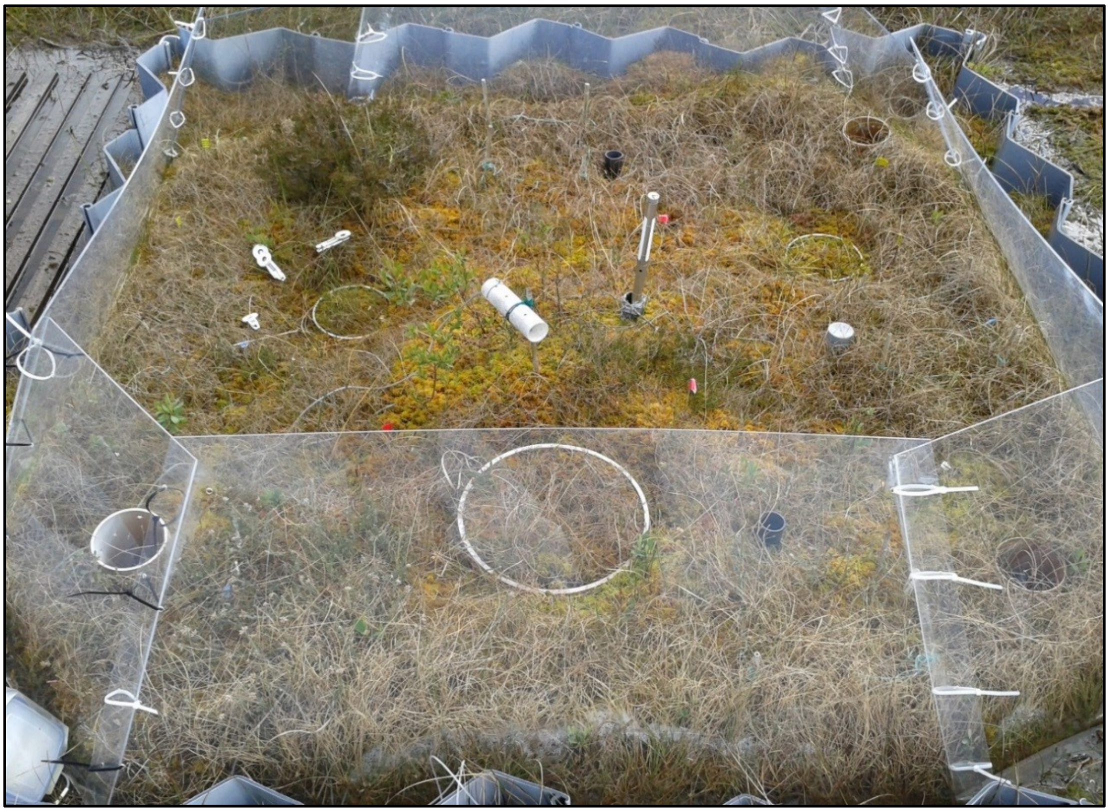


Fig. 4.2. Image of warmed-drought plot (not during experimental period) facing west. The white clips in the upper left corner of the plot are dark adaptation clips for chlorophyll fluorescence measurements. See Fig. 4.1 for annotated schematic.

The experiment reported here ran from in July and August 2014 (6 weeks) consisting of a four-week drought and one week of monitoring before and after this period. Week one was a before drought monitoring phase, during weeks two to five the tubes in the drought and warmed-drought plots were pumped dry, and week six was a subsequent monitoring phase.

For the duration of the drought period (weeks 2-5), the drainage tubes in the plots were maintained at empty with the exception of the 4th-7th of August when depth to water table decreased due to battery failure. This was achieved by daily regulation of the pump programmes and valve settings. Water table levels in the drought and warmed-drought plots were managed by pumping of water from each plot via an automated system (Fig. 4.1). The outflow pipes had holes pre-drilled along their length to allow water to passively flow onto the peatland outside of the plots. Automated data loggers and temperature probes measured air temperature of the within the plots and daily water tables were measured manually via dip-well tubes.

CO_2 fluxes were measured daily within a two-hour period during the middle of the day using the closed chamber method (Dossa et al, 2015) from two fixed position collars within each plot. Vegetation cover within the collars was dominated by *Sphagnum* species (>80%). A factory calibrated EGM-4 Infra-Red Gas Analyser (PP Systems, MA, USA) was used with a transparent CPY-4 chamber for CO_2 flux measurements over 124 seconds. The chamber was uncovered during Net Ecosystem Exchange measurements (NEE) then covered to prevent entry of light during subsequent Ecosystem Respiration measurements (ER). The chamber and gas analyser were flushed for 30 seconds between measurements.

4.3.2 Data analysis

For each gas flux measurement, the highest r^2 for a subset of each measurement time was used to calculate the flux value following Dossa et al (2015). Fluxes with an r^2<85% were analysed visually before deciding upon inclusion or rejection and were calculated using the equation:

$Flux = PV/RTA \times \boldsymbol{\Delta} C/\boldsymbol{\Delta} t$ where;

P= pressure (atm);

V = volume (m^3);

R= gas constant (0.082058 L atm/mol K);

T = temperature (K);

A=surface area of the collar;

$\boldsymbol{\Delta}$C = change in CO_2 concentration (ppm)

$\boldsymbol{\Delta}$t = change in time in hours (number of seconds/60/60).

The Micrometeorological system for gas flux reporting is used here. Ecosystem Respiration (ER measured in the dark) is always a positive value, indicating the movement of CO_2 from the system to atmosphere due to plant (autotrophic) and microbial (heterotrophic) respiration. Gross Primary Productivity (GPP) is always a negative value, calculated from the NEE (light) – ER (dark) values, defined here as the CO_2 fixed by plant photosynthesis. Net Ecosystem Exchange (NEE measured in the light) is the balance of photosynthetic processes (uptake of CO_2 from the atmosphere to the system) and respiration. Positive values indicate the system is a source of carbon to the atmosphere, negative values indicate the system is a sink (Dossa et al, 2015).

A two way mixed effects general linear model was used to test for differences in response variables between treatments with measurement date as the repeated measure and treatment (4 levels) as the fixed factor using SPSS V.22. Univariate general linear models and Bonferroni adjusted Tukey post hoc tests were used for simple and main effects and post-hoc analyses, with significance set at ≤0.05.

4.4 Results

4.4.1 Environmental conditions

Rainfall was sparse during the week prior to instigation of the drought and during the first drought week, which was the period of the highest temperatures (Fig. 4.3). During the drought period there was a significant difference in air temperature between treatments ($F_{(3)}$=12.2, p=0.002), with 25 of the 36 significant post-hoc results reporting significantly higher mean daily air temp in warmed plots then non-warmed (Appendix table 1). Of the 26 drought days, the highest mean daily temp was recorded in the warm-drought plots on 20 days, with the highest temperature of 26.2°C recorded in the warm-drought treatment on 24th of July.

During the drought period, the water table depth of the warmed plots were on average 1.5cm higher (closer to the surface) than control, whilst drought and warm-drought plots were 4.5 and 5.8 cm lower (i.e. deeper) than control respectively (Fig. 4.4), although there were no significant differences between treatments ($F_{(3)}$=3.4, p=0.73). The rise in water table depths in the drought and warm drought treatments between the 4th and 7th of August was due to a combination of rainfall and inadequate pumping regime which was rectified shortly afterwards.

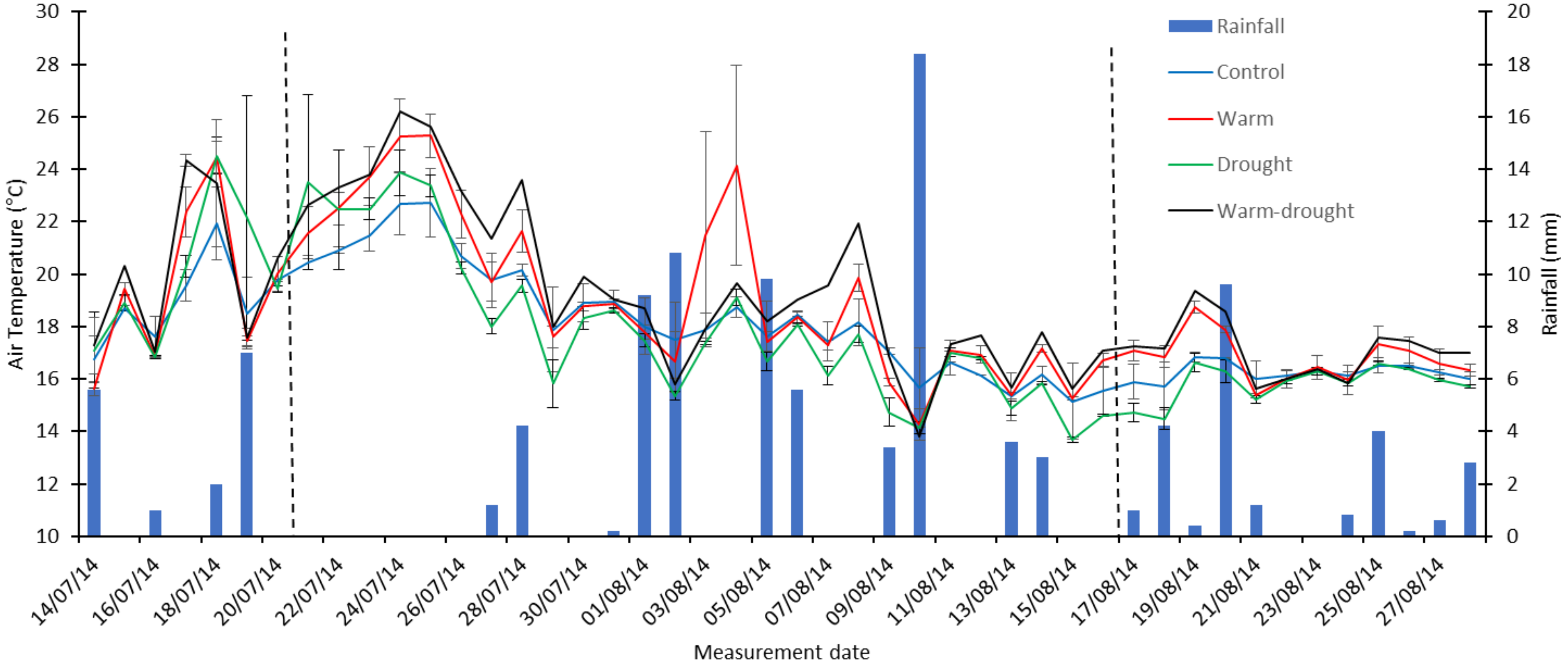


Fig.4.3 Mean daily air temperature in different treatment plots and daily rainfall values at the site. Dashed lines indicate commencement and suspension of artificial drought. Error bars indicate ± one standard error.

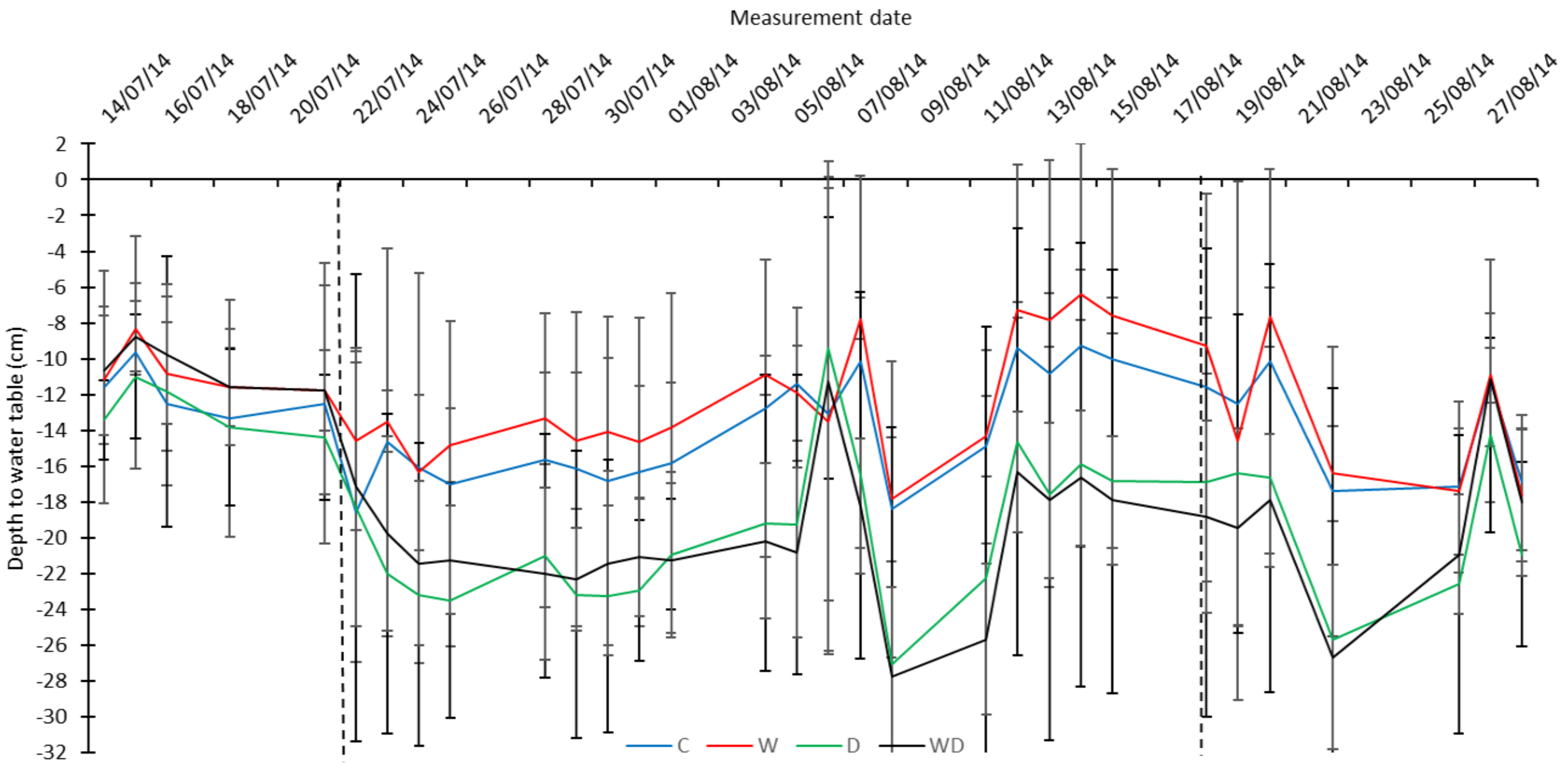


Fig. 4.4 Mean daily depth to water table in the different treatment plots as measured from the surface (cm); Vertical dashed lines indicate the commencement and finishing of active pumping in the drought and warm-drought plots. Error bars indicate ± one standard error.

4.4.2 CO$_2$ fluxes

At the beginning of the drought period, during a period of increasing air temperatures, ecosystem respiration rates (ER) in all treatments showed an increasing trend (Fig. 4.5). However, rates rose most steeply in the warm-drought treatment from 0.6 to 1.0 g CO$_2$ m^{-2} s^{-1}, and from 0.5 to 0.8 g CO$_2$ m^{-2} s^{-1} in the drought treatment, before both declined sharply in line with the control and warmed plots respiration rates (Fig. 4.5). The highest daily mean respiration rates were recorded for six days in the warmed plots and 11 in the warm drought, whilst the lowest were in the non-warmed plots (control 11 days, drought 7 days). The mean ER rates for the drought period were 0.35 (±.05) for control, 0.36 (±.06) for warm, 0.42 (±.07) for warm and 0.48 (±.16) g CO$_2$ m^{-2} s^{-1} for the warm-drought plots. No significant effect of treatment was found on individual days ($F_{(3)}$=.562, p=0.174) or for the cumulative mean for the entire drought period ($F_{(3)}$=2.61, p=0.06; Fig. 4.8). Strong correlations were found between ER and air temperature for the warm, control and warm drought plots (r^2 of 0.67, 0.74 and 0.61 respecively) but were weaker in the drought plots (r^2 0.32). Correllations between ER and WTD were all very low (r^2<0.007).

The highest average daily GPP rate (Fig. 4.6) for the whole of the drought period was in the control plots (0.45 g CO$_2$ m^{-2} s^{-1} ± 0.077) followed by the warm (0.44 ±0.115) drought (0.37 ±0.14) and warm drought plots (0.36 ±0.119). The lowest daily GPP rates were in the drought plots for 18 of the 20 measurement days (6 drought and 12 warm-drought), whilst the most days with the highest mean GPP rates were in the control (13 days) and warm plots (5 days). However, gross primary productivity rates did not demonstrate a significant effect between treatments ($F_{(3)}$=.262, p=.089) nor were there significant differences between cumulative mean GPP for the whole drought period (Fig. 4.8) ($F_{(3)}$=2.27, p=0.09).

The effect of the treatments on the overall net ecosystem exchange (Fig. 4.7) was that the warm-drought treatment had the lowest NEE for the most days during the drought period (18 of 20 days), with a mean of 0.12 g CO_2 m^{-2} s^{-1} (±0.09), whilst the control had the highest NEE for the most days (17 of 20 days), with a daily average of -0.11 g CO_2 m^{-2} s^{-1} (±0.059). Mean daily NEE Flux rates for the warm and drought plots were -0.02 (±0.082) and -0.008 (±0.095) g CO_2 m^{-2} s^{-1} respectively. No significant effect between treatments on individual days was found ($F_{(3)}$=2.9, p=0.098). However, there were significant differences for the overall cumulative mean NEE rates (Fig. 4.8) between treatments ($F_{(3)}$=11.4, p<0.001), with control, warm and drought NEE rates all significantly greater than warm-drought values (p<0.001; p=0.004 and p=0.009 respectively).

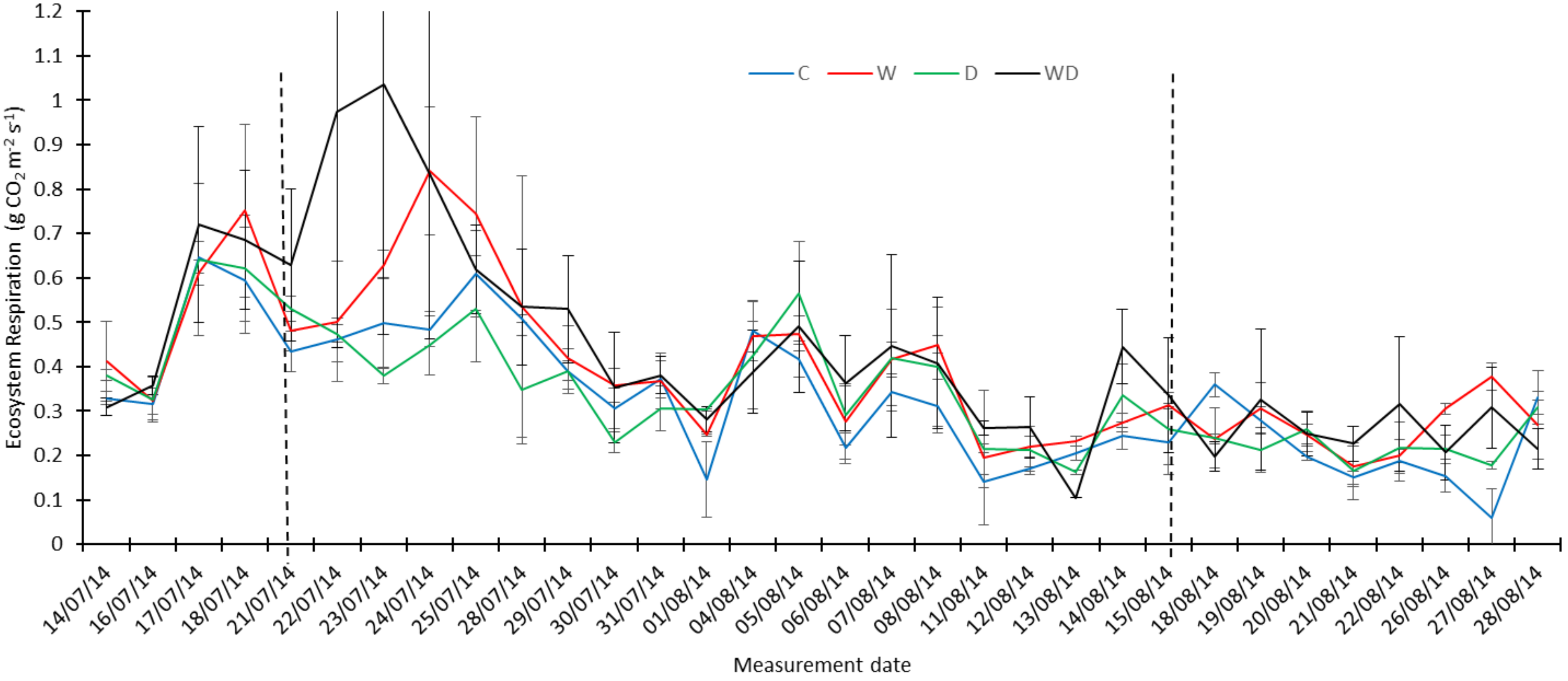


Fig. 4.5 Ecosystem respiration flux rates in the different treatment plots. Vertical dashed lines indicate the commencement and finishing of active pumping in the drought and warm-drought plots. Error bars are ± one standard error.

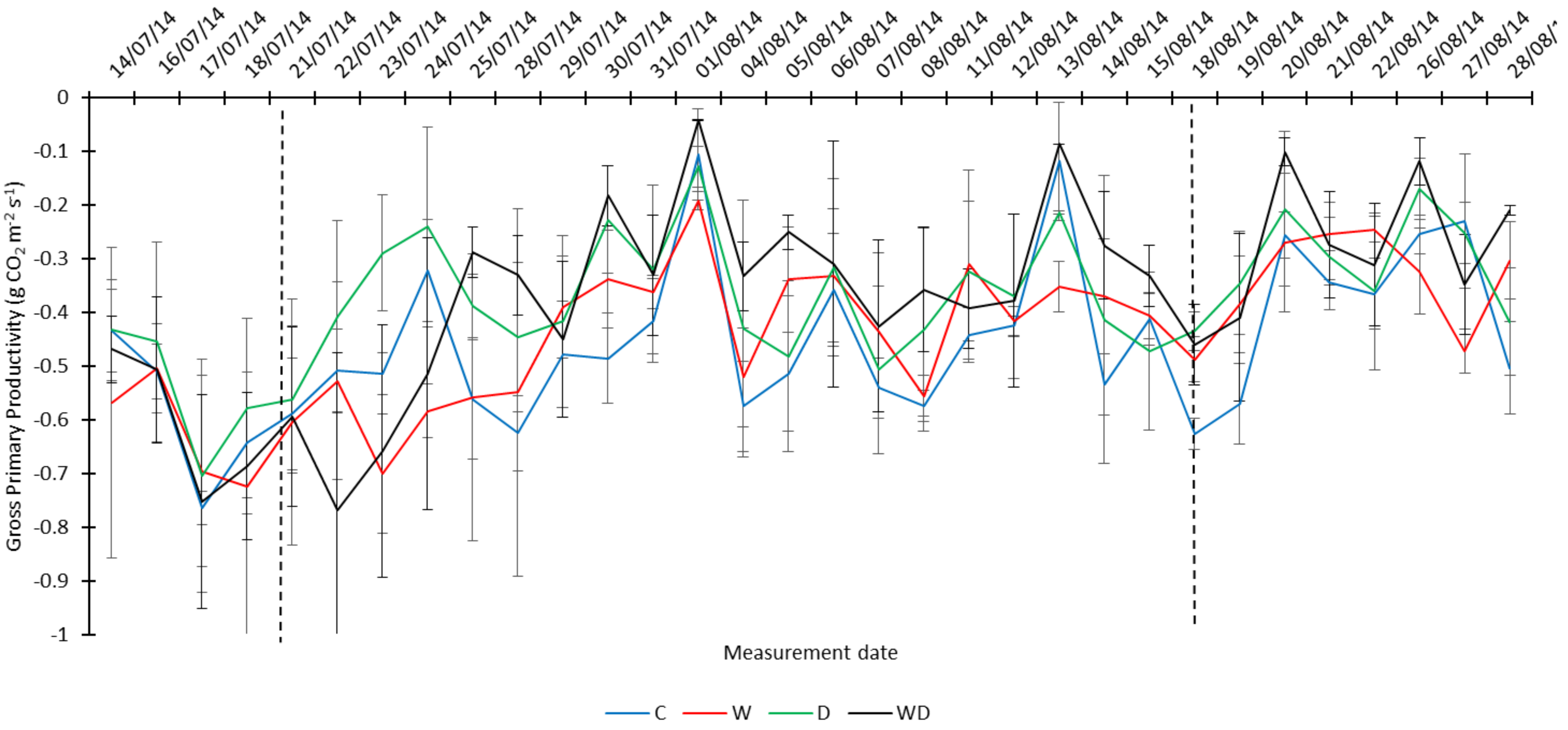


Fig. 4.6 Gross primary productivity flux rates in the different treatment plots. Vertical dashed lines indicate the commencement and finishing of active pumping in the drought and warm-drought plots. Error bars are ± one standard error.

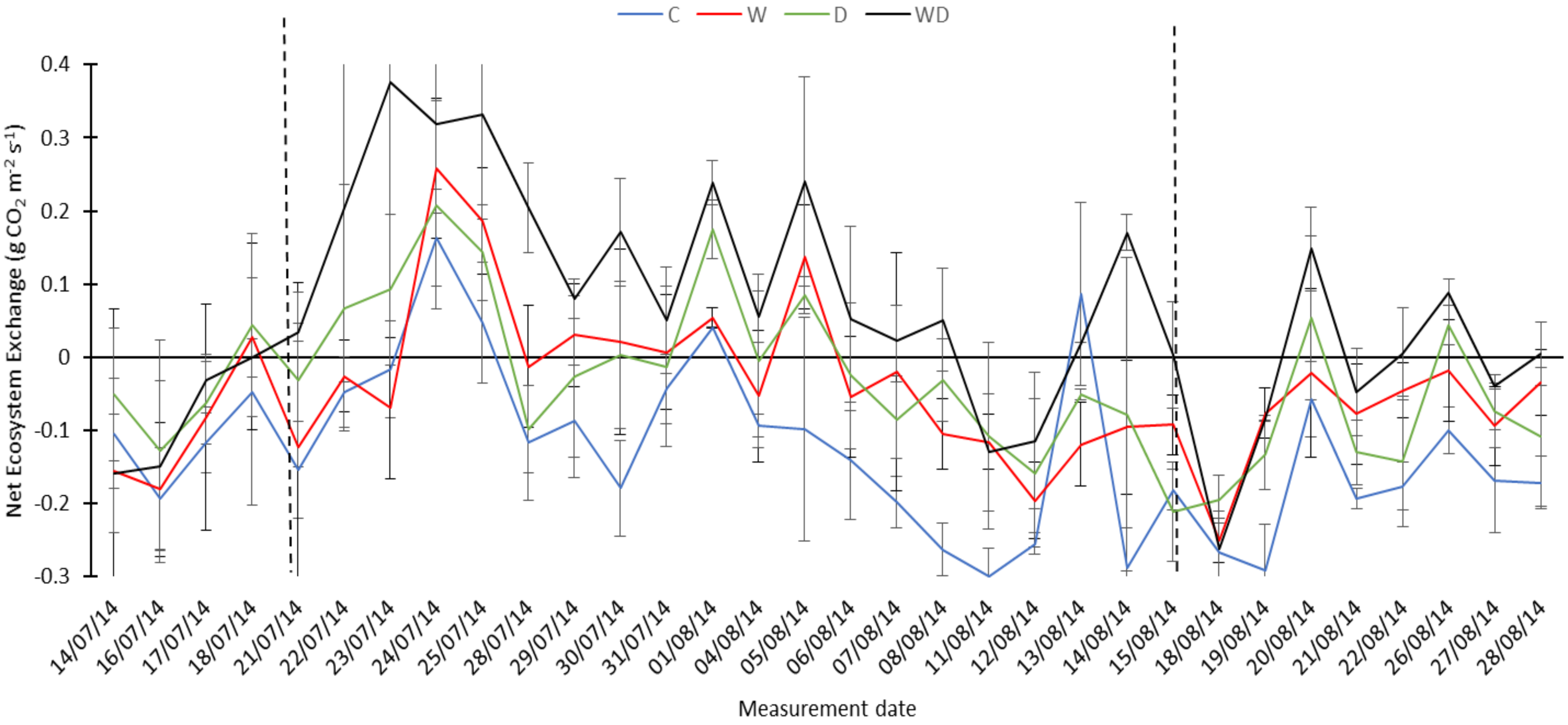


Fig 4.7 Net ecosystem exchange flux rates for the different treatment plots. Vertical dashed lines indicate the commencement and finishing of active pumping in the drought and warm-drought plots. Positive values indicate flux from the peatland to the atmosphere, negative values indicate uptake of CO2 from the atmosphere. Error bars are ± one standard error.

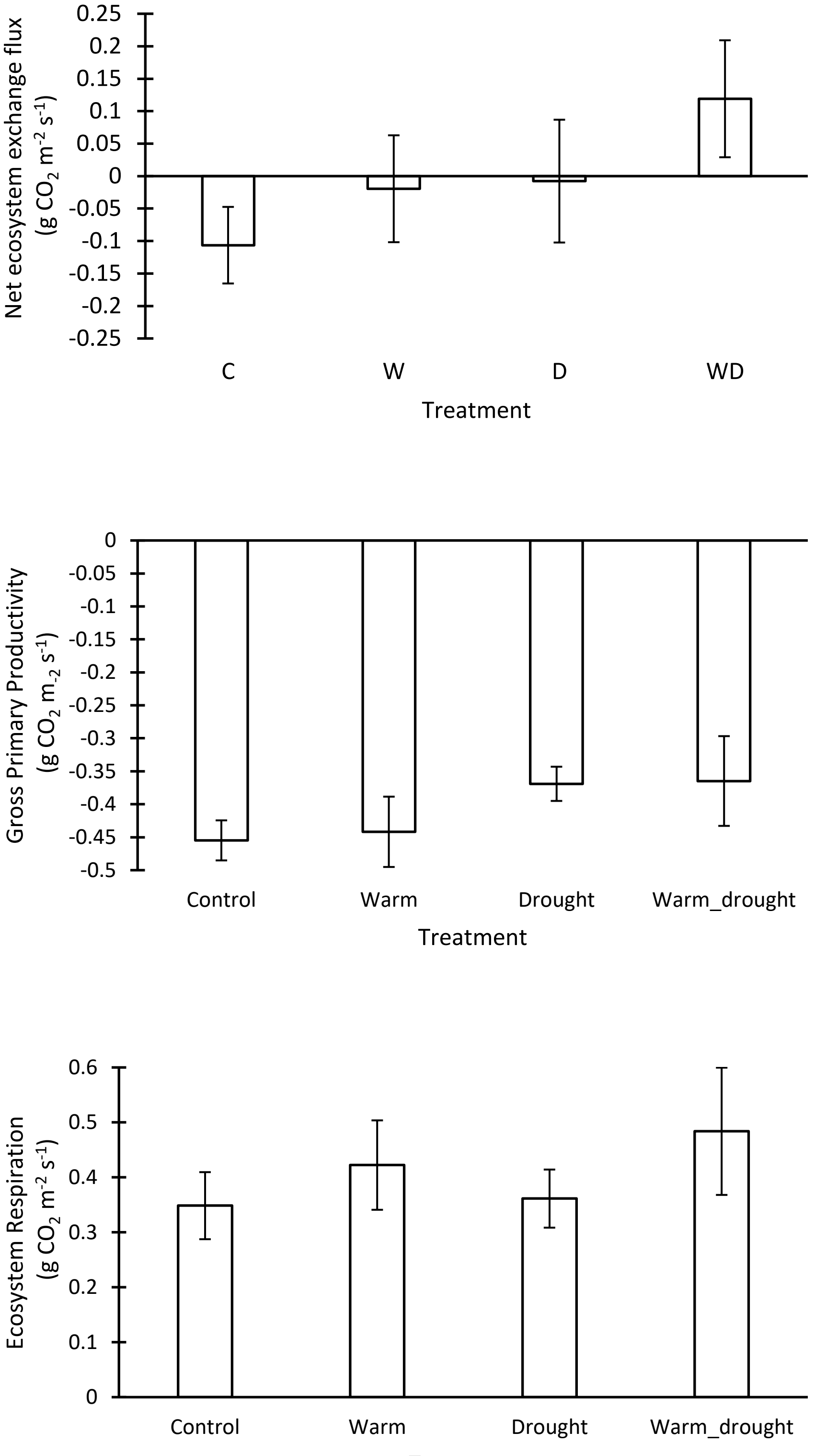


Fig. 4.8 Mean exchange fluxes for the entire drought period for NEE (top), GPP (middle) and ER (bottom). Positive values indicate flux from the peatland to the atmosphere, negative values indicate uptake of CO_2 from the atmosphere. Error bars indicate ± one standard error.

4.5 Discussion

This experiment tested the hypotheses that in conditions of increased air temperatures, short term droughts would lead to; 1) increased ecosystem respiration rates, 2) decreased gross primary productivity rates, resulting in 3) a decrease in net ecosystem exchange rates compared to control.

In accordance with hypothesis 1, the highest mean daily ecosystem respiration rates were most frequently found in the warm-drought plots, followed by the warm plots which suggests that the increase in mean daily air temperature drove the increase in ER rates, particularly as drought alone resulted in decrease in number of days with highest ER. The strongest driver of the ER rate increase appears to have been the warming treatment, as rates increased during the initial pumping phase in the warm treatments but not the drought.

Although the results here were not statistically significant, they are similar to those published in the literature for peatland responses to temperature and drought treatments (Chivers 2009; Pearson 2015). For example, in a two year mesocosm experiment using cores from a *Sphagnum* bog, Updegraff et al (2001) found ER only responded to increases in temperature, with only weak responses when water tables were lowered to -20cm.

Lafleur et al (2005) found similar effects in a five-year study of the effect of natural climatic conditions on an ombrotrophic peatland, with ER rates strongly correlated with air temperature (r^2=.61) but weakly correlated with water table depth (r^2=.26). The authors suggest that this may be due to the Mer Bleue field site being a consistently dry peatland. Though the water table fell in drought years, when it did so it exposed deeper mesotelmic or catotelmic peats which may have been composed of more recalcitrant material than is found in higher, acrotelmic layers (Broder et al 2012). In this study, the relatively high water tables at the start of the experiment would likely have contained acrotelmic peat which had yet to consolidate into catotelmic peat, and thus when exposed to aerobic conditions it led to an initial increase in respiration rates compared to control, exacerbated by the rise in temperatures during the first week of pumping. Reich et al (2009) found this result in an acidic fen when initial drawdown of the water table in an of between 10-20 cm over a six-week period led to an increase in CO_2 ER emissions.

However, droughts alone have also been shown to increase ER rates due to the increased aeration in the acrotelm and surface peat. Lund et al (2012) found ER rates to increase in natural drought events in two separate years that resulted in the peatland acting as a CO_2 source, as opposed to a CO_2 sink in non-drought years. Similarly, Bubier et al (2003) found a 47% increase in ER in a *Sphagnum* peatland when the depth to the water table increased by 10 cm during a dry summer, and Oechel et al (1998) found, over two years, an average reduction of water table depth of 7 cm in a wet sedge fen led to a switch from a CO_2 sink to a CO_2 source.

Gross primary productivity was lowest in both types of drought-affected treatments for the majority of experimental days, driven by the drought treatment, as the warm only treatment resulted in a number of days with GPP higher than control. This concurs with published studies and the second stated hypothesis. Lindroth et al (2007) found a higher sensitivity to temperature for production than respiration in *Sphagnum* dominated boreal mires. Bragazza et al (2016) found that, in a mesocosm transplant experiment, intact *Sphagnum* peat cores exposed to a reduction in precipitation of 60% and increase in mean annual temperature of 5°C increased their ER by 100% whilst soil carbon stores fell by 30%. However, the sink function of the cores still remained, only at a lower rate.

However, it may be that although the lower GPP rates in the warm-drought treatments were predominately due to water table depth, the increase in air temperature contributed to the effect due to increased evaporation from the vegetation surface. Nijp et al (2014) found an increase in depth to the water table resulted in a greater reliance on precipitation (and thus surface moisture) for carbon uptake in *Sphagnum* mosses, as the increase in water table depth reduced the efficiency of capillary action to transport water to the actively growing *Sphagnum* capitula.

In this peatland, the combination of drought in addition to ambient warming resulted in a stronger effect on NEE than warming or drought alone. In a similar experiment, Oechel et al (1998) found in a sedge peatland that drainage of the water table 7 cm below that of control and an increase in temperatures of 0.5°C resulted in an increase in ER and reduced NEE in warm-drought treatments compared to controls. In a *Sphagnum* dominated mesotrophic peatland, Jusczack et al (2011) found, following a modelling approach, that combined WTD and temperature led to an increase in ER of up to 18%.

Future studies on this experimental site focussing on vegetation shifts will contribute to the development of a clearer picture of gas flux responses to expected climate change drivers, in particular assessment of plant functional type responses. For example, although GPP rates measured in plots with *Sphagnum* mosses are lower than those with vascular species (Peichl et al, 2018) they can make a substantial contribution to ecosystem GPP, and further benefit carbon sequestration due to their low decomposability compared to vascular species (Hajek 2009, Van Breemen 1995), their ability to photosynthesise at low light levels (Titus and Wagner 1984), and the associated oxidation of methane due to methanotrophs within the moss layer (Basiliko et al 2004). These effects on peatland biogeochemistry, predominantly due to the presence of *Sphagnum* mosses, and the resultant impacts upon peatland carbon cycling, may be lost if vegetational community shifts lead to dominance of vascular biomass. Furthermore, vascular species in peatlands are more easily mineralised, have higher groundwater demands and can facilitate direct methane transfer to the atmosphere via aerenchymous tissues (Moore et al 2002; Strack et al 2017).

This snapshot of peatland responses to summer drought does not take into account surface moisture and the conditions either side of the experimental period. Antecedent conditions may accentuate the effects of droughts on CO_2 fluxes, shifting a peatland from a CO_2 sink to source (Lund et al 2012). Furthermore, the plots used in this experiment had been subjected to water table drawdown treatments in previous years (2010 and 2012) which were not included in this analysis, nor were the effects of repeated drought years known. Hence; the limited number of replicates available, constrained by suitable sites and logistical demands required to install and maintain field sites of this nature; and the analysis of results for which the experiment was not originally designed for, made the results difficult to ascribe statistical significance to. However, the biological significance of these relatively small changes in environmental conditions should not be ignored.

4.6 Conclusions

Based in the results from this study, it seems reasonable to assume that whilst droughts or a 1-2°C increase in air temperature will diminish the CO_2 sink effect, repeated droughts in raised summer air temperatures will not only reduce this service, but also lead to the enhanced mineralisation and thus release of soil carbon of northern ombrotrophic peatlands to the atmosphere. Consideration should be given to providing moisture to the *Sphagnum* mosses on the peatland surface during warmer and drier conditions, potentially via modern agricultural irrigation methods, in order that gross primary productivity rates mitigate the increased ecosystem respiration rates and maintain a negative overall net ecosystem exchange flux.

4.7 Appendix

Table 1. Statistically significant results for air temperature based on a 2-way General Linear Model and post-hoc Tukey HSD tests. All other values were non-significant. Treatment abbreviations are: C=Control; W=Warm, D=Drought; WD=Warm-Drought.

Date	GLM	Treatments	Tukey *P* value
25/07	$F_{(3)}=5.74$, $p=.021$	C<WD	.034
26/07	$F_{(3}=7.77$, $p=.009$	C<WD	.030
26/07	$F_{(3)}=7.77$, $p=.009$	D<WD	.012
27/07	$F_{(3)}=7.47$, $p=.01$	D<WD	.006
28/07	$F_{(3)}=17.7$, $p=.001$	C<WD	.002
28/07	$F_{(3)}=17.7$, $p=.001$	D<W	.034
28/07	$F_{(3)}=17.7$, $p=.001$	W<WD	.049
28/07	$F_{(3)}=17.7$, $p=.001$	D<WD	.001
30/07	$F_{(3)}=4.72$, $p=.035$	D<WD	.027
06/08	$F_{(3)}=23.3$, $p<.001$	C<WD	.005
06/08	$F_{(3)}=23.3$, $p<.001$	W<WD	.002
06/08	$F_{(3)}=23.3$, $p<.001$	D<WD	<.001
07/08	$F_{(3)}=26.0$, $p<.001$	C>D	.045
07/08	$F_{(3)}=26.0$, $p<.001$	C<WD	.003
07/08	$F_{(3)}=26.0$, $p<.001$	W<WD	.002
07/08	$F_{(3)}=26.0$, $p<.001$	D<WD	<.001
08/08	$F_{(3)}=32.5$, $p<.001$	C<W	.029
08/08	$F_{(3)}=32.5$, $p<.001$	C<WD	<.001
08/08	$F_{(3)}=32.5$, $p<.001$	D<W	.005
08/08	$F_{(3)}=32.5$, $p<.001$	W<WD	.011
08/08	$F_{(3)}=32.5$, $p<.001$	D<WD	<.001
09/08	$F_{(3)}=41.0$, $p<.001$	W<C	.005
09/08	$F_{(3)}=41.0$, $p<.001$	D<C	<.001
09/08	$F_{(3)}=41.0$, $p<.001$	D<W	.005
09/08	$F_{(3)}=41.0$, $p<.001$	W<WD	.013
09/08	$F_{(3)}=41.0$, $p<.001$	D<WD	<.001
12/08	$F_{(3)}=38.4$, $p<.001$	C<W	.002
12/08	$F_{(3)}=38.4$, $p<.001$	C<D	.009
12/08	$F_{(3)}=38.4$, $p<.001$	C<WD	<.001
12/08	$F_{(3)}=38.4$, $p<.001$	W<WD	.004
12/08	$F_{(3)}=38.4$, $p<.001$	D<WD	.001
14/08	$F_{(3)}=69.2$, $p<.001$	C<W	.001
14/08	$F_{(3)}=69.2$, $p<.001$	C<WD	<.001
14/08	$F_{(3)}=69.2$, $p<.001$	D<W	<.001
14/08	$F_{(3)}=69.2$, $p<.001$	W<WD	.019
14/08	$F_{(3)}=69.2$, $p<.001$	D<WD	<.001

Chapter 5

Impacts of warming, drought and sea level rise on ombrotrophic peatlands: a synthesis

5.1 Synthesis

The impetus for this work was the lack of evidence about how peatland carbon gas fluxes respond to climate change drivers, specifically seawater flooding, and the combined effects of long-term increases in air temperature with summer droughts. Given the dramatic losses of these ecosystems to peat harvesting, land use change, the large volume of carbon in peat, and the potential for the sequestration from or release to the atmosphere of gaseous carbon, studies such as these are critical in advancing our understanding of how peatlands and the atmosphere will interact in the predicted climate change trajectory.

Observations in both the lab and field study here support earlier published evidence (Wilcox 1984; Pouliot 2013) that bryophytes, and in particular *Sphagnum*, are relatively sensitive to seawater or salinity compared with vascular land plants. Since bryophytes are often the dominant vegetation of peat bogs, it is likely that this habitat is particularly vulnerable to seawater flooding. The effects of seawater are likely to lead to physiological damage in *Sphagnum* mosses, though responses may be species or niche-specific. Both photosynthesis and chlorophyll fluorescence were inhibited in both species *Sphagnum pulchrum* and *S. cuspidatum*, indicating damage was sustained to the photosynthetic apparatus. However, the weaker effect of seawater on the *S. pulchrum* locally dominant species (at Cors Fochno), suggests that this species may possess greater resilience to seawater flooding events. Published studies have identified inter and intra-specific differences in tolerance of seawater in other mosses (Bates et al 2009; Bates and Brown 1975), and this may be the case in *Sphagnum* mosses.

In a field setting, the chlorophyll fluorescence responses were dissimilar from the laboratory experiment, and *Sphagnum* plants were physically distinct in their coloration and fragmentation from the earlier indoor study. Furthermore, recovery was evident within a year following application of the treatment in the field. This highlights the importance of verifying laboratory experiments in optimum conditions, which should be viewed as 'potential' responses, with experiments in natural field settings. Reasons which may account for the failure of the chlorophyll fluorescence measurements to show differences between treatments in the field using the same hollow-dwelling *Sphagnum* species from the laboratory experiment include; operator error, particularly when used in bright sunshine when light may have seeped into the clips and attenuated the readings; or the inappropriateness of the method in field conditions, as most studies employing this method are in laboratory or glasshouse conditions. Alternatively, another, as yet unidentified factor, such as moisture content, may have interacted with the treatment and diminished the effect on the mosses photosystem II apparatus.

Whilst acknowledging the limited size of the plots used in the field experiment, and the method of vegetation analysis employed, there was a limited longer-term effect of seawater on the vegetational composition of the plots. When combined with the inhibition of methane exchange to the atmosphere, and the maintenance of negative net ecosystem exchange fluxes throughout the experiment, these results raise an interesting dilemma for environmental managers. In the face of almost certain future sea level rise and increased frequency of storm surges (Wong et al 2014; Rahmstorf

2007), when balancing the demands of maintaining and improving peatlands for their own intrinsic value; against the extrinsic, anthropogenic ecosystem service viewpoint of peatlands acting as atmospheric carbon sinks and stores; it may become necessary to consider whether managed seawater flooding during periods of high temperatures and water scarcity may be a beneficial strategy if CO_2 emissions to the atmosphere are to be restricted. This has already been suggested for peatlands converted to agricultural use in order to minimise mineralisation of peat and subsidence during drought periods (Brouns et al 2014).

Using the results from this study as a pilot study, a larger scale experiment, utilising peatland areas already identified as likely to be flooded by natural events, knowledge of total peatland carbon budgets and changes in vegetational communities can be gained, with additional consideration for the duration floodwaters remain in the peatland, the concentration of salts within the seawater, and the frequency of re-flooding events.

In the study of the effect of combined increased mean annual air temperature and summer droughts, the combination of these conditions resulted in the shift from the peatland being a carbon source to becoming a carbon sink during the experimental drought period. Future studies on this site will investigate how these short-term responses affect the annual carbon budget of peatlands, but these short-term event-specific data may also provide support for management decisions when these conditions occur. As previously mentioned, the addition of seawater can inhibit both primary productivity and ecosystem respiration fluxes, as well methane emissions which can account for 18% of the emission of carbon taken up by peatland as gross primary productivity (Rinne et al 2018).

From the results from this study, increases in mean annual temperature or increased frequency of drought events will result in reduced net ecosystem exchange, due to increases in both heterotrophic and autotrophic respiration if adequate water is not available for the moss layer. If water tables deepen due to drought combined with warmer conditions, the potential exists for the development of positive net ecosystem exchange for gaseous CO_2 fluxes, due to exposure of peats to oxygen and higher temperatures than when they are in anaerobic conditions (Liu et al 2016). However, if precipitation is available to maintain a moist surface, and thus a suitable water content for the *Sphagnum* mosses, this may be avoided by an increase in gross primary productivity (Nijp et al 2014). However, the duration and timing of a drought have been shown to be important factors in peatland carbon budgets (Lund et al 2012), which highlights the benefit of long term datasets derived from field experiments which can capture the variation in environmental conditions.

5.2 Research and management opportunities

Future studies could be directed towards identifying to what extent *Sphagnum* species (or populations) demonstrate tolerance or resistance to acute or chronic exposure to seawater. This research could be applied in the management of coastal or estuarine peatlands at risk of seawater flooding, by relocating and transplanting mosses into niche based on salinity to which they are better adapted. It would be advisable to measure responses of a secondary control group which is not immersed in any treatment water, but which has rainwater applied to maintain water content, as very high water content can also lower photosynthesis rates (Maseyk et al 2009). In addition, bryophyte species that are naturally found within a range of where airborne marine derived salts are deposited may provide a useful test of saline resistance. Given the carbon accumulation potential of Sphagna, the maintenance of these species should be of primary concern in order to promote a negative carbon budget for peatland sites (i.e. remaining carbon sinks). However, if *Sphagnum* bryophytes prove to be unsuitable for at risk coastal peatlands, particularly if the duration and frequency of flooding events increases, then consideration should be given to other bryophytes which have already been shown to possess saline tolerance. However, their interactions with the peat substrate, in particular their ability to effectively cap the carbon store, and also their ability to suppress vascular plant expansion would require investigation prior to implementation of this strategy.

Although the reduction in the respiratory emissions of CO_2 and CH_4 observed in the seawater flooding experiment may be viewed beneficially by land managers in terms of their carbon emissions budgets, this must be weighed against the large inhibition of CO_2 uptake in photosynthesis. In order to understand the consequences of seawater inundation on the overall carbon budget, a more detailed and regular measurement series would be required. This would need to consider fluvial carbon losses and identify how antecedent conditions affect gaseous fluxes and vegetation responses in subsequent years.

Using the results from this study as a pilot study, a larger scale experiment, utilising peatland areas already identified as likely to be flooded by natural events, knowledge of total peatland carbon budgets and changes in vegetational communities can be gained, with additional consideration for the duration floodwaters remain in the peatland, the concentration of salts within the seawater, and the frequency of re-flooding events.

The extent and distribution of coastal peatlands at risk of seawater flooding in the UK is currently unknown, and would be a beneficial desk based exercise in order to determine potential carbon losses from the peat store, but also short-term changes in gaseous carbon fluxes.

In these studies, realistic and relevant climatic drivers of change affected the carbon exchange characteristics of a maritime ombrotrophic peatland. If trends in climate continue, and predictions are realised, it is likely that the carbon budgets of these relatively rare ecosystems on the edge of their temperate European bioclimatic envelope will be changed, with potential changes in vegetation communities, and ultimately feeding back into the global climate cycle, depending upon the intensity of the environmental drivers.

Chapter 6 References

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