Land/atmosphere carbon dioxide exchange at semi-natural and regenerating

peatlands in East Anglia, UK

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Abstract

This thesis presents the first direct flux measurements of land/atmosphere carbon dioxide (CO₂) exchange at managed lowland peatlands in the East Anglian Fens, UK. The dynamics and magnitude of land/atmosphere CO₂ exchange were quantified at semi-natural and regenerating ex-arable fens located at the Wicken Fen Nature Reserve in Cambridgeshire. Eddy covariance measurements were made at the semi-natural fen throughout two thermally and hydrologically dissimilar periods during 2009 and 2010, and at the regenerating former-arable fen over the complete annual cycle of 2010. The study sites were characterised by strong seasonal variation in CO₂ exchange. The seminatural fen was a net source of 85.47±25.78 g CO₂-C m⁻² between 20th March and 31st December 2009, and a small net sink of -22.66±18.85 g CO₂-C m⁻² for the same period of 2010. Photosynthesis and ecosystem respiration were both higher during warm conditions of 2009 compared to 2010, but enhanced rates of ecosystem production were outweighed by large CO₂ losses during warm and dry conditions in autumn. The large interannual variability in CO₂ exchange illustrates the sensitivity of semi-natural fens to climatic variability and change, and highlights the need to maintain high water levels to prevent large losses of soil carbon to the atmosphere as CO₂. The regenerating fen functioned as a small net source of 21.24±17.11 g CO₂-C m⁻² yr⁻¹. On the basis of values currently used to represent CO₂ losses from arable fens, the annual CO₂ balance for the ex-arable fen in 2010 indicates the net CO₂ benefit of fenland rehabilitation was an avoided loss of -87.7±17.11g CO₂-C m⁻² yr⁻¹. The results from the regenerating site imply that a more adaptive water management strategy will be needed if the environmental conditions required for peat formation and net carbon capture are to be restored.

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 measurement site

Abbreviations and notation

AGDD	Accumulated growing degree days (°C)
amsl	above mean sea level (m)
BF	Bakers Fen
С	Carbon
С	Width of a Gaussian curve
СЕН	Centre for Ecology and Hydrology
CH_4	Methane
CO_2	Carbon dioxide
DOC	Dissolved organic carbon
EBC	Energy balance closure
EC	Eddy covariance
EF	Emission factor
E _o	Activation energy/temperature sensitivity (K)
ER	Ecosystem respiration
ER _{max}	Maximum ER (μ mol CO ₂ m ⁻² s ⁻¹)
EVI	Enhanced vegetation index
EVI _{max}	Maximum EVI
f	Relative footprint contribution
F_c	Land/atmosphere flux
Fs	CO ₂ storage flux
G	Soil heat flux (W m ⁻²)
GHG	Greenhouse gas

GMT	Greenwich mean time
GPP	Gross primary production
GPP ₁₅₀₀	GPP at 1500 μ mol PAR m ⁻² s ⁻¹
GPP _{opt}	Optimal rate of photosynthesis under non- limiting conditions (μ mol CO ₂ m ⁻² s ⁻¹)
Н	Sensible heat flux (W m ⁻²)
H ₂ O	Water
IPCC	Intergovernmental Panel on Climate Change
IRGA	Infrared gas analyser
ITT	Integral turbulence test
JD _{max}	Julian day maximum
k	Level of PAR where GPP is 50% of its maximum rate
k	von Karman's constant (0.4)
LAI	Leaf area index $(m^{-2} m^{-2})$
LAI _{max}	Maximum LAI (m ⁻² m ⁻²)
LE	Latent heat flux (W m ⁻²)
LSU	Livestock units
MDC	Mean diurnal cycle
MDS	Marginal distribution sampling
MODIS	Moderate resolution Spectroradiometer
Ν	Nitrogen
n	Number of data points
N ₂ O	Nitrous oxide
NECB	Net ecosystem carbon balance

NEE	Net ecosystem CO ₂ exchange
NIR	National GHG Inventory Report
NNR	National Nature Reserve
NPP	Net primary production
Р	Precipitation (mm)
PAR	Photosynthetically active radiation (μ mol photons m ⁻²)
POC	Particulate organic carbon
QC	Quality control
R	Average monthly ER (μ mol CO ₂ m ⁻² s ⁻¹)
R ₁₀	Basal ER at 10°C
r^2	Determination coefficient
R _g	Global radiation (W m ⁻²)
RMS	Root mean square error
R _{net}	Net radiation (W m ⁻²)
SAC	Special Area of Conservation
SAT	Sonic anemometer-thermometer
SCAS	Sunscan Canopy Analysis System
SD	Standard deviation
SOM	Soil organic matter
SSSI	Site of Special Scientific Interest
T _{air}	Air temperature (°C)
To	Temperature where ER reaches zero (°C)
T _{opt}	Optimal temperature (°C)
T _{peat}	Peat temperature (°C)

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T _{ref}	Reference temperature (10°C)
T_{tol}	Temperature tolerance (°C)
и	Mean horizontal wind speed (m s^{-1})
<i>u*</i>	Friction velocity (m s ⁻¹)
UK	United Kingdom
UNFCCC	United Nations Framework Convention on Climate change
UoL	University of Leicester
VPD	Vapour pressure deficit (HPa)
W	Vertical wind speed (m s ⁻¹)
WF	Wicken Fen
WL	Water level (cm)
WL _{max}	Maximum water level (cm)
WL _{opt}	Optimal water level (cm)
WL _{tol}	Water level tolerance (cm)
WSF	Wicken Sedge Fen
X ₁	Upwind distance from tower (m)
X _{max}	Peak footprint distance from tower (m)
Zm	Measurement height (m)
α	Ecosystem apparent quantum yield (μ mol PAR μ mol photons ⁻¹)
θ_{peat}	Volumetric peat moisture content (m ⁻³ m ⁻³)
ρ	Spearman's correlation coefficient

Chapter One: Introduction

1.1 Background

Climatic warming threatens to disrupt the continuing welfare of human socioeconomic systems and the functioning of the natural and semi-natural ecosystems upon which it depends (UNFCCC, 1992; Stern, 2007). Rising concentrations of atmospheric greenhouse gases¹ (GHGs) have resulted in a 0.6° C increase in mean global surface temperature since the pre-industrial period (Solomon *et al.*, 2007). The global temperature rise could reach 1.4 to 5.8° C by 2100 (Solomon *et al.*, 2007). The magnitude of the impacts associated with climate warming will depend on the timing and efficacy of measures taken to reduce emissions and stabilise atmospheric GHG concentrations (Stern, 2007; House *et al.*, 2008; UNEP, 2010). Assessments have shown decisive and early mitigation action is required if the worst environmental and societal impacts of climate change are to be avoided, and the economic costs of adaptation minimised (Stern, 2007; Ciscar *et al.*, 2010).

Anthropogenic climate change is driven by the accumulation of GHGs in the atmosphere (Solomon *et al.*, 2007; Canadell *et al.*, 2010). This largely reflects the balance between GHG emissions from human economic activity, and removal of atmospheric CO₂ by biospheric (i.e. oceanic and terrestrial) sinks (House *et al.*, 2008; Canadell *et al.*, 2010; Raupach & Canadell, 2010). After fossil fuel combustion, land use and land use change represent the second largest source of anthropogenic GHG emissions (Le Quéré *et al.*, 2009; Raupach & Canadell, 2010). At the same time, the terrestrial biosphere currently removes around one third of CO₂ emitted during fossil

¹ Greenhouse gases are the gaseous constituents of the atmosphere that positively influence the Earths radiative balance. The three primary GHGs are the biogenic gases: carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O).

fuel combustion (Canadell *et al.*, 2007), slowing the rate of atmospheric CO_2 growth (Raupach *et al.*, 2008), and representing one of the most fundamental services provided by the Earth system (Obersteiner, Böttcher & Yamagata, 2010).

Evidence from observational and modelling studies suggests the strength of the biospheric sink could be weakening (Cox *et al.*, 2000; Canadell *et al.*, 2007; Le Quéré *et al.*, 2009; Raupach *et al.*, 2008). If persistent, this decline could accelerate the rise in atmospheric CO₂ concentration and climate warming (Canadell *et al.*, 2010). As such, improved management of the various elements of the land biosphere has been identified as one key option for near-term climate change mitigation (Lal, 2004; Smith *et al.*, 2010b; Obersteiner, Böttcher & Yamagata, 2010). This could be achieved either by manipulating ecosystems (and agri-systems) for enhanced carbon (C) capture and storage, or by preventing C losses from large and vulnerable C reservoirs, such as peatlands (Smith *et al.*, 2010b; Obersteiner, Böttcher & Yamagata, 2010). Moreover, improved knowledge on the dynamics of terrestrial C sinks/sources is required for (i) predictions of future climates (Cox *et al.*, 2000); (ii) identifying GHG and temperature stabilisation pathways (House *et al.*, 2008; Meinshausen *et al.*, 2009; UNEP, 2010); and (iii) designing climate change mitigation policies (Canadell *et al.*, 2010).

Peatlands are wetland ecosystems that store disproportionately large amounts of soil C relative to other terrestrial ecosystems (Gorham, 1991; Limpens *et al.*, 2007). Globally, peatlands cover approximately three percent of the global land surface, but are estimated to store up to one third of terrestrial organic C (Gorham, 1991; Turanen *et al.*, 2002). The large peatland C pool reflects a positive net imbalance between organic C assimilated during photosynthesis, and the release of carbon dioxide (CO_2) and

methane² (CH₄) during organic matter decomposition (Frolking & Roulet, 2007). Net accumulation of peat and the long-term stability of the large amounts of C stored in peatlands are facilitated by the perennially saturated (and anaerobic) soils that define these environments (Holden, Chapman & Labadz, 2004).

In Europe and elsewhere, large tracts of peatland have proved vulnerable to a range of pressures, including: drainage for agriculture, forestry and peat extraction (Joosten & Clarke, 2002; Byrne *et al.*, 2004; Holden, Chapman & Labadz, 2004). In some regions, land use changes and/or climatic shifts have reduced or reversed the peatland C sink capacity (Oechel *et al.*, 2000; Janssens *et al.*, 2005; Page *et al.*, 2011). In particular, peatland drainage has contributed significantly to atmospheric C loading by destabilising peatland soil C stocks and releasing large quantities of historically accumulated soil C to the atmosphere in the form of CO_2 (Lohila *et al.*, 2004; Couwenberg, 2011, Couwenberg *et al.*, 2011).

Fens are minerotrophic peatlands of high conservation status due to their large soil C stocks and often high species diversity (Lamers *et al.*, 2002; Warrington et al., 2009; Natural England, 2010). In temperate Europe, much of the original area of lowland fen habitat has been drained and is now degrading under agricultural land use (Byrne *et al.*, 2004; Holden, Chapman & Labadz, 2004; Baird, Holden & Chapman, 2009). CO_2 emissions from drained and cultivated boreal and temperate peats are amongst the highest from any type of agri-ecosystem, globally (Lohila *et al.*, 2004; Couwenberg *et*

 $^{^{2}}$ CH₄ is a greenhouse gas with a global warming potential 25 times greater than CO₂ on a 100-year basis. By definition, CO₂ has a global warming potential of one on a 100 year basis.

al., 2011). In countries with large areas of cultivated peatland, CO_2 (and nitrous oxide³ - N₂O) emissions from this source contribute significantly to national-scale GHG emissions (Janssens *et al.*, 2005; Schaller, Kantelhardt & Drösler, 2011). Furthermore, agricultural use of peatlands has resulted in significant land surface subsidence (Hutchinson, 1980), and has been a major driver of biodiversity loss (Couwenberg *et al.*, 2011).

The East Anglian Fenland of the East of England (The English Fens or The Fens) contains the largest contiguous area of lowland fen peatland in the British Isles (Baird, Holden & Chapman, 2009). Prior to the seventeenth century, the Fenland (Figure 1.1) contained a *circa* 1480 km² topogeneous mire complex in the low-lying basin surrounding The Wash (Burton & Hodgson, 1987; Friday, 1997; Moore, 1997). Wet conditions for peat formation were maintained by regular flooding by the Fenland Rivers (Figure 1.1) and irregular marine incursions (Moore, 1997). Widespread drainage, followed by agricultural intensification from the seventeenth century onwards has reduced the area of semi-natural (i.e. relatively intact) fen habitat to approximately 7.13 km² (Stroh *et al.*, 2012). These areas are largely contained within the boundaries of four small nature reserves⁴ located towards the periphery of the Fenland basin (Moore, 1997; Figure 1.1). Collectively, these fragmented sites represent some of the most biologically diverse areas in the UK (Warrington *et al.*, 2009).

 $^{^3}$ N_2O is a greenhouse gas with a global warming potential 298 times greater than CO_2 on a 100-year basis.

⁴ The four Fenland Nature Reserves are located at Wicken Fen, Holme Fen, Woodwalton Fen and Chippenham Fen. Each is characterised by distinct floral and faunal assemblages and differences in land management practices (Moore, 1997). These reserves are amongst the most biologically diverse ecosystems in the United Kingdom. Wicken Fen has the largest species list for any site in England with over 8000 recorded species (Warrington *et al.*, 2009).



Figure 1.1: Map of the East Anglian Fenland. The map shows the approximate extent of minerotrophic peatland in the region, the four Fenland Rivers and the location of the four main Fenland nature reserves. Source: Friday (1997). Image reproduced with copyright permission from Apollo Books.

The modern Fenland landscape is dominated by intensive production of cereals and row crops (Morris *et al.*, 2010). Drained peat soils in the region are amongst the most productive and profitable for food production in the UK (Morris *et al.*, 2000; Morris *et al.*, 2010), but simultaneously represent one of the largest sources of land use related

GHG emissions (Thompson, 2008; Natural England, 2010; Worrall *et al.*, 2011). Concerns over the future of the Fenland biodiversity are driving efforts to restore large tracts of agriculturally degraded fen habitat in areas surrounding existing nature reserves (Hughes *et al.*, 2011; Stroh et al., 2012). Collectively, two landscape-scale wetland restoration projects in the Fenland aim to restore over 80 km² of agricultural land by 2100 (The National Trust, 2007; The Great Fen Project, 2012). A significant proportion of this proposed restoration activity will target agriculturally degraded peat soils.

Until recently, peatland management and restoration activity has been aimed primarily at nature conservation (Holden *et al.*, 2008; Birkin *et al.*, 2011). Concern over maintaining and/or enhancing terrestrial C capture and storage is now generating considerable interest from scientists, land managers and policymakers concerned with exploiting land-based options with the potential to mitigate CO_2 (and other GHG) emissions (Thompson, 2008; Natural England, 2009; Birkin *et al.*, 2011). In the UK, this translates into a growing effort to protect and (where possible) enhance existing peatland soil C stocks (Natural England, 2010). Moreover, activities with potential to positively influence ecosystem GHG budgets and protect biodiversity have significant potential for linking the objectives of these globally recognised concerns (Smith, 2012).

Landscape-scale fenland rehabilitation will have implications for land/atmosphere exchanges of water, energy and GHGs (Byrne *et al.*, 2004). It is generally assumed fenland rehabilitation will result in net GHG benefits, primarily due to the scale of avoided CO_2 (and N_2O) emissions and/or renewed peat formation and net C sequestration (Gauci, 2008; Natural England, 2010; Couwenberg, 2011; Morris *et al.*,

2010). At the current time, the magnitude of any such CO_2 benefit remains largely unquantified (Byrne *et al.*, 2004; Höper *et al.*, 2008; Baird, Holden & Chapman, 2009; Worrall *et al.*, 2011).

It is imperative to gain a broader understanding of the dynamics and magnitude of land/atmosphere CO_2 (and non- CO_2 GHG) exchanges within the wider framework of ecosystem service provision before policies focused on C-orientated land management are enacted (Lloyd, 2006; Ostle *et al.*, 2009). Furthermore, improved understanding of the mechanisms driving land/atmosphere CO_2 (and other GHG) exchange is prerequisite for effectively managing peatland environments and their large soil C reserves under a changing environment (Glenn *et al.*, 2006).

The micrometeorological eddy covariance (EC) technique has emerged as a principal tool for quantifying vertical exchanges of water, energy and biogenic GHGs (i.e. CO_2 , CH_4 and N_2O) between the atmosphere and biosphere at ecosystem scale (Baldocchi, 2003, Law & Verma., 2004; Aubinet, Vessala & Papale, 2012). As of 2012, EC is deployed at over 500 sites within the framework of the global FLUXNET (2012) initiative, providing unprecedented insights into the functioning of the various elements of the terrestrial biosphere (Baldocchi *et al.*, 2001).

At the current time, EC studies at managed temperate peatlands are rare (Couwenberg, 2011; Teh *et al.*, 2011). In a UK context, very limited EC (or other) flux data exist on C (and GHG) fluxes for any type of lowland fen. No (UK) data presently exist for fens that are regenerating after restoration from intensive arable land use (Baird, Holden & Chapman, 2009). With large areas of degraded fen habitat due to come out of

agricultural production (Friday & Colston, 1999; The National Trust, 2007), these gaps in data and knowledge must be systematically addressed.

1.2 Aim and research questions

This research forms part of FENFLUX, a collaborative project between the University of Leicester and the Centre for Ecology and Hydrology (CEH), Wallingford. FENFLUX aims to quantify water, energy and C fluxes from semi-natural, agricultural and regenerating fens in East Anglia using micrometeorological techniques. Only the net ecosystem exchange of CO_2 (NEE) is considered in this thesis. Water and energy fluxes were presented by Kelvin (2011). A combined analysis of energy, water and CO_2 fluxes will be presented on completion of the individual projects. CO_2 fluxes from agricultural fens were not obtained as part of the data collection for this thesis, but are currently being researched by this author and colleagues (Morrison *et al.*, submitted).

The aim of this thesis is to improve current knowledge of the dynamics and magnitude of land/atmosphere CO_2 exchange at semi-natural and regenerating former arable fens in East Anglia. EC flux measurements are reported for two managed fens at the Wicken Fen National Nature Reserve in Cambridgeshire. EC measurements were made at a semi-natural reference site during two thermally and hydrologically dissimilar periods in 2009 and 2010, and at a regenerating former arable fen for the complete annual cycle of 2010.

The research represents the first EC CO_2 measurements to be obtained at managed peatlands in East Anglia, and the first to quantify land/atmosphere CO_2 exchange at a regenerating temperate ex-arable fen. The thesis aims were to: (i) quantify and compare the seasonal pattern of net ecosystem CO_2 exchange (NEE) at semi-natural and regenerating fens; (ii) diagnose the main factors influencing NEE and its component fluxes; and (iii) provide estimates of the magnitude of land atmosphere CO_2 exchange at the two managed peatlands.

The thesis addresses the following questions:

- 1. What are the main factors influencing land/atmosphere CO₂ exchange at seminatural and regenerating fens?
- 2. What is the seasonal pattern of land/atmosphere CO₂ exchange at semi-natural and regenerating fens? How does the seasonal pattern of land/atmosphere CO₂ at regenerating fens compare to semi-natural fens?
- 3. What is the magnitude of land/atmosphere CO_2 exchange at semi-natural and regenerating fens (are these ecosystems sinks or sources for atmospheric CO_2)?
- 4. What are the C cycle impacts of landscape-scale fenland rehabilitation in East Anglia? The importance of quantifying all C and GHG fluxes is acknowledged; here, this question is addressed with specific attention to CO₂.

The results are aimed at improving knowledge on the current and potential future role of lowland fens in terms of the UK land C budget. The results will help identify which factors are likely to influence the CO_2 balance of lowland peatland environments, providing information for improved land management in a region that is projected to experience significant climatic variability and change over the coming century (UKCIP, 2009).

Results from the regenerating fen are aimed at providing a first estimate of the magnitude of any annual CO_2 emissions reduction resulting from arable fen rehabilitation. This will provide an important first step towards improved C (and GHG) accounting from managed and regenerating fens. The results will help improve the evidence base required for inclusion of managed peatlands under UK commitments to meeting reporting requirements of domestic and international agreements on climate change mitigation, such as the UK Climate Change Act (2008) and The Kyoto Protocol⁵ (1998) to the United Nations Framework Convention on Climate Change (UNFCCC, 1992).

1.3 Specific objectives

The specific objectives of this research are:

 To install and maintain an eddy covariance flux tower at a regenerating former arable fen and maintain it over a complete annual cycle. The EC tower at the seminatural site was installed and maintained by researchers from CEH, Wallingford.
 CO₂ exchange measurements for the semi-natural site were provided in exchange for evapotranspiration data from the regenerating fen site.

⁵ As well as any future legally-binding or voluntary international agreements on climate change mitigation following the first commitment period (2008 to 2012) of the Kyoto Protocol that remain under negotiation at the Conference of Parties to the UNFCCC.

- 2. To develop EC data handling protocols. This objective is subdivided to include: (i) post-processing of EC measurements; (ii) development of site-specific data quality control (QC) procedures; (iii) filling of unavoidable data gaps in the EC flux records; (iv) evaluation of the plausibility of the EC flux measurements; and (v) statistical partitioning of EC measurements of NEE into its component fluxes (i.e. CO₂ assimilation during photosynthesis and total CO₂ efflux via ecosystem respiration).
- 3. To characterise the meteorological and hydrological conditions observed over the study period. Where possible, to compare observed conditions with longer-term climatic patterns in the Fenland region.
- 4. To analyse and compare seasonal changes in measured land/atmosphere CO_2 exchange and its component fluxes at the two peatland sites. At the semi-natural fen, EC measurements obtained during contrasting conditions in 2009 and 2010 facilitates an analysis of between-year differences in land/atmosphere CO_2 exchange.
- 5. To analyse the main factors influencing land/atmosphere CO_2 exchange and its component fluxes at semi-natural and regenerating fens. This objective is based on the analysis of estimates of gross primary production derived from the statistical partitioning of NEE (from objective 2), and analysis of nocturnal EC CO_2 flux measurements (i.e. for periods when photosynthesis is inactive).

- 6. To quantify the magnitude of land/atmosphere CO_2 exchange and its component fluxes at the semi-natural and regenerating fen sites at daily, monthly, seasonal (at the semi-natural fen) and annual (at the regenerating fen) timescales. This objective is subdivided to include: (i) integration of measured and gap-filled flux densities at daily, monthly seasonal and annual timescales; and (ii) quantification of the uncertainty in time-integrated estimates of net ecosystem CO_2 exchange.
- 7. To provide a first-order estimate of the magnitude of any CO_2 benefits resulting from landscape scale Fenland restoration in East Anglia. This objective includes: (i) a literature survey to identify the most appropriate estimate of the current scale of CO_2 emissions from drained and cultivated peatlands in the Fenland; (ii) identification of the current and projected area of fen peatland currently under restoration management in the area surrounding the study site; and (iii) comparison of the annual CO_2 balance from the regenerating site with the best estimate of CO_2 emissions from arable fens.

1.4 Thesis structure

The remainder of this thesis is structured as follows. Chapter 2 (Scientific and policy background) reviews the scientific and policy literature relevant to this research. Chapter 3 provides an overview of the theory and application of EC technique. In Chapter 4 (Materials and methods), the flux measurement sites, EC instrumentation and ancillary datasets, together with all EC data handling protocols are described. Chapter 5 (Environmental conditions) summarises the environmental conditions encountered over the study period.

The CO_2 flux measurements from the two managed fens are presented in Chapters 6 and 7. Chapter 6 (Seasonal change and factors influencing land/atmosphere CO_2 exchange) presents an analyses of the seasonal change in NEE and its component fluxes. An analysis of the main environmental factors influencing the measured CO_2 exchange is provided. Chapter 7 (CO_2 budgets of semi-natural and regenerating fens) presents time-integrated estimates of the magnitude of land/atmosphere CO_2 exchange at the two study sites. In chapters 5 and 6, results from the semi-natural peatland are initially presented and compared for the 2009 and 2010 measurement periods. Results from the regenerating fen are presented and contrasted with the semi-natural site during the paired measurement period of 2010.

Chapter 8 (Discussion and conclusions) presents a discussion of the results presented in previous chapters. Results are discussed in light of the research questions posed by this research. Limitations of the current research are identified and discussed alongside potential avenues for extended and/or future research activity. The final part of Chapter 8 summarises the contributions of this work towards knowledge of C cycling in lowland temperate peatlands and provides a synopsis of the main findings of this thesis.

Chapter Two: Scientific and policy background

This chapter reviews the scientific and policy literature relevant to this research and highlights the knowledge gaps addressed by this work. The chapter begins by describing the importance of peatlands in terms of C storage and climate. The physical and biological processes operating in peatland ecosystems and their relevance to the peatland C budget are outlined. The current state of knowledge relating to CO₂ fluxes in minerotrophic fens is reviewed. The impacts of the drainage and agricultural use of fens peatlands is discussed. The magnitude of C loss from cultivated fens is reviewed to identify the CO₂ emissions factor most appropriate to conditions in the study area. The scientific and policy-relevant literature pertaining to C cycle processes in restored lowland fen peatlands is summarised. The chapter concludes with a summary of current knowledge and data gaps, and how this research will contribute towards addressing them.

2.1 Peatlands: definitions

The term peatland encompasses a diverse range of peat-forming wetlands located in regions from the arctic to the tropics (Limpens *et al.*, 2008). The defining characteristics of natural peatland environments are groundwater levels that are at or close to the surface throughout the year, and the presence of an organic soil formed by the progressive accumulation of partially decomposed organic matter, or peat.

The most commonly used peatland classification is based on water balance and hydrochemistry (Table 2.1). Bogs are ombrogenous (i.e. precipitation-fed) peatlands, whereas minerotrophic peatlands (fens) are sustained by precipitation together with inputs of base-rich (alkaline) waters of telluric origin (Glenn *et al.*, 2006; Sonnentag *et*

al., 2009). As such, fens are often a characteristic feature of topographically confined lowlands (Baird, Holden & Chapman, 2009). These hydrological and hydrochemical differences are reflected by differences in dominant plant functional types (Glenn *et al.*, 2006). Differences in plant communities are in turn reflected by differences in the physiochemical characteristics of the accumulated peat layer and associated C dynamics (Limpens *et al.*, 2008; Sulman *et al.*, 2010).

Table 2.1: Characteristics of ombrogenous (bogs) and minerotrophic (fen) peatlands in the United Kingdom

Peatland type	Characteristics
Ombrogenous	Ombrogenous peatlands (or bogs) are dependent on meteoric inputs of water and nutrients. Bogs are acidic (pH ~4) and nutrient poor (Holden, Chapman & Labadz, 2004). <i>Sphagnum</i> sp. mosses are the dominant peat forming species. Ombrogenous peatlands are further classified as blanket (upland) and raised (lowland) bogs (Baird, Holden & Chapman, 2009).
Minerotrophic	Minerotrophic peatlands (or fens) receive meteoric inputs together with base-rich waters that have been influenced by contact with mineral soils. Fens are classified along a pH gradient, ranging from poor (pH 4.5 to 5) to intermediate (pH 5 to 7) to extreme-rich (pH 6.8 to 8) fens, reflecting the relative influence of minerotrophic versus meteoric inputs (Worrall <i>et al.</i> , 2011). Poor fens may support <i>Sphagnum</i> sp. mosses, whereas rich fens tend to support vascular plant communities. In the UK, the dominant types of minerotrophic peatland are basin and floodplain fens (Baird, Holden & Chapman, 2009). Prior to the onset of drainage in the seventeenth century, The East Anglian Fenland was formed of a mosaic of floodplain and basin fens (Baird, Holden & Chapman, 2009).

2.2 Peatlands: carbon storage and climate

Peatlands, like all terrestrial ecosystems, are coupled to the atmosphere via two mechanisms. Land surface elements interact with the atmosphere by way of biophysical processes, including albedo effects, and turbulent exchanges of momentum and sensible (H) and latent heat (LE) (Chapin *et al.*, 2000; Heimann & Reichstein, 2008). Terrestrial ecosystems also influence (and are influenced by) climate through their role in global biogeochemical cycles, notably via exchanges of the biogenic GHGs: CO₂, methane

CH₄ and N₂O (Chapin *et al.*, 2000; Heimann & Reichstein, 2008). Biophysical processes act more strongly at local scales (Jackson *et al.*, 2008), whereas biogeochemical exchanges act globally as GHGs become well-mixed throughout the atmosphere (Pongratz *et al.*, 2010).

The existence of large peat deposits demonstrates peatlands have functioned as a large net sink for atmospheric C over past millennia (Lafleur, Roulet & Admiral, 2001). Depending on location, peatlands have been accumulating atmospheric C (as peat) for 6000 to 10,000 years (Lafleur, Roulet & Admiral, 2001). C accumulates as peat as cool and wet subsurface conditions favour net primary production (NPP) over organic matter decomposition (Glenn *et al.*, 2006; Cai *et al.*, 2010). At the same time, wet conditions required for net C accretion are conducive to production of the potent GHG CH₄ (Levy *et al.*, 2012), some of which may be emitted to the atmosphere (Limpens *et al.*, 2008).

In general, peat formation rates reflect low rates of decomposition rather than high ecosystem productivity (Lafleur, Roulet & Admiral, 2001, Cai *et al.*, 2010; Sottocornola & Kiely, 2010). This is not universally true, however, as reed-dominated (and tropical) wetlands represent some of the most productive ecosystems, globally (Brix, Sorrell & Lorenzen, 2001; Zhou, Zhou & Jia, 2009; Rocha & Goulden, 2009). Evidence from peat cores suggest long-term peat accumulation rates range from 15 to 30 g C m⁻² yr⁻¹, regardless of peatland type (Turanen *et al.*, 2002; Strilesky & Humphreys, 2012). Globally, persistent rates of peat formation has resulted in a estimated peatland C pool of 200 to 455 Pg C concentrated on *circa* 3% of the land area (Gorham, 1991; Limpens *et al.*, 2008). At the higher end of this range, the peatland C

pool equates to around one third of all^6 soil organic C, making these ecosystems the highest density C pool within the land biosphere.

Northern peatlands (those above 45°N) are presently thought to exert a net cooling effect on global climate as the effect of long-term C capture and storage (i.e. net cooling) outweighs CH₄ emissions (i.e. net warming) over time (Frocking & Roulet, 2007). However, the future of the large amounts of C stored as peat is of major concern, as changes in C fluxes to and from this large C reservoir due to destabilisation by climatic and/or land use change has significant potential to influence atmospheric C loading and global climate (Baird, Holden & Chapman, 2009). Increased release of gaseous C from peatlands in response to climatic warming represents an additional risk of a positive feedback to anthropogenic climate change (Sagerfors *et al.*, 2008; Sottocornola & Kiely, 2010).

2.2.1 Peatlands in a UK context

Peatlands represent single largest component of the UK land C stock (Dawson & Smith, 2007; Ostle *et al.*, 2009). At UK level, Scottish ombrogenous peatlands dominate in terms of area and C storage (Billett *et al.*, 2010). The situation changes when English peatlands are considered, with (deep and wasted) fens dominating peatland in terms of area and C storage (Table 2.2). As with other UK ecosystems (i.e. forests), peatlands have been extensively converted to productive land uses, resulting in net losses of C to the atmosphere (Thompson, 2008). In a recent review, Worrall *et al.* (2011) estimated UK peatlands are currently a net source of 5.73 Mt CO_{2e} yr⁻¹. Of this, more than half of

⁶ The global soil organic carbon pool is approximately 1500 Pg C (Smith, 2004).
the total GHG emissions were attributed to drained and cultivated lowland fens in England.

Table 2.2: Estimates of peatland area total C storage by peatland type in England (modified from Natural England, 2010).

Peatland type	Area (Km ²)	Carbon (Mt C)	% of total peatland C
Blanket bog/upland valley mire	3553	138.0	24%
Raised bog	357	57.5	10%
Lowland fen/reedbeds (deep)	958	144.0	25%
Lowland fen/reedbeds (wasted)	1922	186.4	32%
Shallow peaty soils	5272	58.5	10%
Total	6790	584.4	-

Notes: Deep peat soils are areas with a peat layer more than 40 cm in depth. Shallow peat soils are areas with a peat layer less than 40 cm. Wasted peats are those that have been extensively degraded by drainage and cultivation and are now influenced by underlying mineral substrates (Natural England, 2010). This definition differs from the one used in UK GHG accounting, where deep and shallow peats are defined on the basis of a 1 m depth criterion (Choudrie *et al.* 2009).

2.3 Carbon cycling in peatlands

The peatland C cycle can be conceptualised as an intricate balance between a number of interacting pools and fluxes (Figure 2.1 and Table 2.3). In naturally functioning (i.e. relatively intact) peatlands, atmospheric CO_2 is reduced to carbohydrate (biomass) during photosynthesis (gross primary production - GPP). A proportion of this assimilated C (*circa* 40 to 50%) is used to support the growth and metabolic activity of plants and mycorrhizae (if present) and is rapidly cycled back to the atmosphere as CO_2

(Dawson & Smith, 2007; Smith *et al.*, 2010a). The remaining net primary production (NPP) provides the primary source of organic C supporting all other biological processes and associated C fluxes (Dawson & Smith, 2007), and the total amount of C potentially available for long-term storage as peat (Byrne *et al.*, 2004).

NPP enters the soil environment where it is decomposed by heterotrophic microorganisms (Dawson & Smith, 2007). Depending on redox conditions in the nearsurface environment, organic matter (root exudates, litter and peat) is decomposed along one of two main biogeochemical pathways: CO₂ is produced and released when aerobic (oxic) conditions prevail, whereas slow decomposition under strictly anaerobic (anoxic) conditions favours CH₄ production (Limpens *et al.*, 2008; Levy *et al.*, 2012). Long-term storage of C as peat occurs as a small (and variable) fraction of NPP enters storage under saturated (i.e. anaerobic) conditions below the permanent water table (Byrne *et al.*, 2004). Additional losses/gains of organic (and inorganic) C occur laterally and vertically along hydrological pathways (Dinsmore *et al.*, 2010), and laterally via aeolian transport (Warburton, 2003).





Figure 2.1: Diagrams illustrating the carbon cycle of (a) naturally functioning and (b) drained and agriculturally used peatlands. In the natural case (a), the water level fluctuates seasonally and the oxic peat layer may/may not always be present. In the drained case (b), the oxic layer is artificially increased, although anoxic conditions may still be present below the drainage level. Blue and brown ovals represent aerobic and anaerobic soil microbial populations, respectively. See main text and Tables 2.3 and 2.4 for descriptions of processes and controlling factors. Images modified from Page *et al.* (2011). Copyright permission provided by Dr. Chris Malins of the International Council on Clean Transportation.

At the current time, studies of net ecosystem C balance (NECB; Table 2.2) are rare for peatland environments (e.g. Hendricks *et al.*, 2007; Roulet *et al.*, 2007; Nilsson *et al*, 2008; Koehler, Sottocornola & Kiely, 2011; Dinsmore *et al.*, 2010). The results of available studies suggest natural (or at least relatively undisturbed) peatlands are generally a net C sink to a small net C source, but with large interannual variations in individual flux terms and NECB (Roulet et al., 2007; Limpens *et al.*, 2008). In most studies, the components of the peatland NECB (or GHG balance) are considered individually (e.g. Warburton, 2003; Sagerfors *et al.*, 2008; Strack *et al.*, 2008; Levy *et al.*, 2012). As the focus of this research is the land/atmosphere exchange of CO₂ (NEE).

Table 2.3: Summary of peatland carbon flux terminology and key environmental controls

Carbon flux term Description and summary of environmental controls Gross primary Photosynthesis (GPP) represents the primary source of organic carbon in peatland (and other) ecosystems. At site scale, dominant controls on GPP are production (GPP) nutrient status and ecology, which in turn control ecosystem phenology and plant productivity (Lindroth et al., 2007). Key abiotic controls on ecosystem photosynthesis rates are: irradiance, air and peat temperature, water levels and soil moisture availability; and stomatal responses to atmospheric vapour pressure deficit (Riutta et al., 2007a, Shurpali et al., 2009; Sulman et al., 2010). A fraction of the CO₂ fixed during photosynthesis is used to support the growth and metabolic requirements of plants and root-associated mycorrhizae Autotrophic (if present). Approximately 50% of the C fixed during photosynthesis is cycled back to the atmosphere during autotrophic (or dark) respiration respiration (Dawson & Smith, 2007; Smith et al., 2010a). The magnitude of autotrophic respiration is tightly coupled to the photosynthetic activity of plants via the supply of recently assimilated photosynthates, and is strongly regulated by temperature (Cai et al., 2010). Net primary NPP is the amount of biomass remaining after accounting for the CO₂ released during autotrophic respiration. It is defined as: NPP=GPP-R_a. NPP represents the potential source of organic material available for peat formation (Dawson & Smith, 2007; Smith et al., 2010a). production (NPP) Heterotrophic CO₂ is released during the heterotrophic decomposition of plant litter, root exudates and peat by soil microorganisms under aerobic conditions (Cai et al., 2010). The main controls on heterotrophic respiration rates are the quality and quantity of available organic substrates (i.e. plant and root litter, respiration root exudates, peat), regulated by the growth and metabolic activity of microbial communities in response to temperature and soil moisture and/or water levels (i.e. via influences on redox conditions) (Limpens et al., 2008; Parmentier et al., 2009; Leifeld, Steffens & Galego-Sala, 2012; Hatala et al., 2012). CO₂ produced during heterotrophic decomposition of peat is transported to the atmosphere via diffusion. Total soil respiration describes the total CO₂ efflux released (and measureable at the soil surface, i.e. using a chamber). Total soil respiration includes: Total soil respiration (i) CO₂ released by autotrophic respiration in the rhizosphere (i.e. by plant roots and mycorrhizae), and (ii) heterotrophic decomposition of root exudates, plant and root litter and peat when aerobic conditions prevail in the near-surface environment.

Table 2.3 continued. Summary of peatland carbon flux terminology and key environmental controls

Description and summary of environmental controls Carbon flux term Ecosystem Ecosystem respiration (ER) represents the sum of all vertical CO₂ effluxes resulting from autotrophic (plant) and heterotrophic (microbial) respiration respiration (ER) (Reichstein et al., 2005a; 2012). It includes the autotrophic respiration of the aboveground parts of plants and the total soil respiration (see above). In the absence of photosynthesis (i.e. during nocturnal periods), ER is the quantity that is directly measured using the eddy covariance technique (Chapter 3). In undisturbed peatlands, ER is typically the second largest of the peatland C transfers after GPP (i.e. assuming a net CO₂ sink). Studies on ER in peatlands have highlighted the importance of the developmental stage and metabolic activity (i.e. autotrophic respiration) of plant communities (e.g. Cai et al., 2010), temperature (e.g. Lafleur et al., 2005) and water levels (e.g. Shurpali et al., 1995; Lloyd, 2006; Hatala et al., 2012) and/or soil moisture (e.g. Parmentier et al., 2009) as key controls on overall ecosystem respiration rates. Net ecosystem CO₂ The net ecosystem exchange of CO₂ (NEE) represents the dynamic balance between GPP and ER. NEE is typically the largest of the net C fluxes on a mass basis. NEE is the quantity directly measured using the eddy covariance technique (Chapter 4), and is defined as: NEE=ER-GPP, where positive exchange (NEE) values indicate losses of CO_2 to the atmosphere, negatives the reverse. Integration of NEE defines the CO_2 sink/source status of an ecosystem over a given timeframe (i.e. daily, monthly, seasonal or (inter)annual). Methane (CH_4) is produced by (heterotrophic) methanogenic Achaea under strictly anaerobic conditions and consumed by methanotrophic Achaea Methane (CH_4) under oxic conditions (Levy et al., 2012). CH₄ can be transported to the atmosphere by diffusion, episodic ebullition, and via transport through aerenchyma of some vascular wetland plants (Brix, Sorrell, & Lorenzen, 2001). CH₄ production is controlled by the quality and quantity of organic substrates, (i.e. litter, root exudates), water levels, temperature, and by the presence/absence of vascular plants (i.e. in terms of root exudates production and plant transport). (Levy et al., 2012). Lateral/vertical losses of C occur as dissolved and particulate organic C (DOC/POC) via fluvial pathways. DOC losses may be an important Dissolved/particulate component of the peatland C balance under some conditions (Billett et al., 2010; Dinsmore et al., 2010). Lateral transfers of DOC/POC are important organic carbon in the landscape scale redistribution of organic C. DOC/POC may be lost to the atmosphere as CO₂/CH₄ via evasion downstream of peatland (DOC/POC) environments. Particulate losses/gains of C also occur via wind erosion (Warburton, 2003). The net ecosystem carbon balance (NECB) of a peatland is the net accumulation/loss of C after balancing all other losses/gains of C (Chapin et al., Net ecosystem carbon balance 2006; Lovett et al., 2006). (NECB)

2.4 Net ecosystem CO_2 exchange

The vertical land/atmosphere exchange of CO_2 (i.e. the NEE) is typically the largest and most variable flux component of the peatland NECB (Roulet *et al.*, 2007; Nilsson *et al.*, 2008). NEE reflects a dynamic balance between the opposing fluxes of gross primary production (GPP) and ecosystem respiration (ER), each process governed by a number of environmental controls (Table 2.3 & Figure 2.1). In this thesis, NEE is defined using the micrometeorological sign convention, where negatives indicate net CO_2 uptake by the ecosystem. As NEE includes the main C fluxes which add (GPP) and remove (ER) organic C from peatlands (Sagerfors *et al.*, 2008), its value must be negative (and in excess of all other C losses) over time if net C accretion is to be maintained (Page *et al.*, 2011). Furthermore, as the largest of the C flux terms, quantification of NEE is typically taken as the first stage in constructing a more comprehensive C (or GHG) balance (Jacobs *et al.*, 2007).

In naturally functioning (i.e. relatively intact) peatlands, most of the C fixed during photosynthesis is respired back to the atmosphere in the form of CO_2 (Chimner & Cooper, 2003b; Dawson & Smith, 2007). As GPP and ER are strongly regulated by thermal and hydrological regimes (Table 2.3), even small changes to one/both of these large (and opposing) fluxes can have strong implications for the CO_2 sink/source status of a peatland (Chimner & Cooper, 2003b; Glenn *et al.*, 2006; Cai *et al.*, 2010).

Multi-year studies of NEE in peatlands have shown warmer conditions and/or lowering of water levels can shift the balance towards more positive NEE or net losses of CO_2 (Alm *et al.*, 1999; Shurpali *et al.*, 1995; Bubier *et al.*, 2003; Cai *et al.*, 2010). Such a response may reflect increases in ER (e.g. Shurpali *et al.*, 1995; Alm *et al.*, 1999;

Bubier *et al.*, 2003; Cai *et al.*, 2010), reductions in GPP (e.g. Griffis *et al.*, 2000; Sonnentag *et al.*, 2010; Leppälä *et al.*, 2011) or a combination of the two (e.g. Aurela *et al.*, 2007; 2009). Conversely, other studies have shown that extended growing seasons, and warmer and/or drier conditions (i.e. lower water levels and/or soil moisture) can stimulate ecosystem production, thereby compensating for higher CO_2 efflux rates (Sulman *et al.*, 2009; 2010; Flanagan & Syed, 2011). Although not a comprehensive list of potential responses to environmental variability, such contrasting results demonstrate the need for improved knowledge of C dynamics across a range of peatland types in order to quantify the current and potential future role of peatlands within the Earth system (and to regional/national C budgets).

Peatland studies show high spatial (i.e. within and between-site) and temporal (i.e. seasonal and interannual) variability in NEE (e.g. Bubier *et al.*, 2002; Lindroth *et al.*, 2007; Riutta *et al.*, 2007a; 2007b; Schrier-Uijl *et al.*, 2009; Teh *et al.*, 2011). To date, most studies of land/atmosphere CO₂ exchange at (minerotrophic) peatlands have focussed on near-pristine ecosystems of the arctic, sub-arctic and boreal climates (Limpens *et al.*, 2008). In terms of (northern) fens, annual estimates of NEE range from a net gain of -189±47 g CO₂-C m⁻² yr⁻¹ (Flanagan & Syed, 2011) to net losses of 100 g CO₂-C m⁻² yr⁻¹ (Saarnio *et al.*, 2007; Limpens *et al.*, 2007), although most studies report annual values within a narrower range (e.g. Aurela *et al.*, 2002; 2004; 2009; Riutta *et al.*, 2007a; 2007b; Nilsson *et al.*, 2008; Sagerfors *et al.*, 2008).

In contrast, fewer studies have reported NEE at temperate peatland environments (e.g. Nieveen *et al.*, 2005; Lloyd, 2006; Hendricks *et al.*, 2007; Jacobs *et al*, 2007; Veenendaal *et al.*, 2007; Teh *et al.*, 2011; Hatala *et al.*, 2012). Most temperate peatlands

typically show some degree of anthropogenic modification (Billett *et al.*, 2010; Natural England, 2010). As such, process knowledge and estimates of flux magnitudes gained from near-pristine (i.e. northern) mires is unlikely to reflect the dynamics of CO_2 exchanges operating in managed temperate peatlands (Teh *et al.*, 2011). Results from available studies at managed temperate fens show higher overall CO_2 flux rates compared to more northerly sites, annual estimates of NEE ranging from -466 to *circa* 220 g CO_2 -C m⁻² yr⁻¹ for (cool temperate) sites with permanent vegetation cover (range from Hendricks *et al.*, 2007; Jacobs *et al.*, 2007; Table 8.1). These higher values reflect warmer temperatures and longer thermal growing seasons compared to more northerly locations (Teh *et al.*, 2011), as well as the influences of land management practices.

An increasing number of studies have reported estimates of NEE for UK (and Irish) peatlands (e.g. Worrall *et al.*, 2003; Billet *et al.*, 2010 and references therein; Dinsmore *et al.*, 2010; Sottocornola & Kiely, 2010; Koehler, Sottocornola & Kiely, 2011). Thus far, UK peatland research has focused almost exclusively on ombrogenous peatlands. For example, lowland fens were not mentioned in a recent review of UK peatland C budgets (Billet *et al.*, 2010), despite their importance in terms of land C storage (see Table 2.2) and net GHG emissions (Worrall *et al.*, 2011).

Only one previous study has reported NEE for any type of lowland fen in the UK. Lloyd (2006) reported a grazed and mown fen in the Somerset Levels was a small net source of 59 g CO₂-C m⁻² yr⁻¹ during a single year of measurements (after accounting for biomass removal). As such, the current CO₂ sink/source status of fens in the UK (and East Anglia in particular), and those under different management regimes remain largely unquantified. Other C fluxes have yet to be systematically addressed.

Quantification of the dynamics and magnitude of C cycle processes operating in seminatural/managed/restored lowland fens in the UK has been identified as a major gap in data and knowledge (Baird, Holden & Chapman, 2009) and a priority area for research (Evans *et al.*, 2011; Worrall *et al.*, 2011). The micrometeorological CO_2 flux measurements reported in this thesis therefore represent the first stage towards filling these important gaps, increasing the number of available UK lowland fen CO_2 flux datasets by a factor of three.

2.5 Agricultural impacts

Although not considered directly as part of the data collection for this research⁷, it is important to review the impacts of agricultural land use on peatland ecosystems and associated CO_2 (and non- CO_2 GHG) dynamics. This provides the basis for estimating potential CO_2 savings presented by landscape scale fenland regeneration in East Anglia. This section summarises changes to peatland ecosystems brought about by drainage and (mainly arable) cultivation, and reviews the current state of knowledge on the magnitude of CO_2 emissions from fens under arable land use.

Agricultural use of peatlands (b in Figure 2.1) is limited by surface wetness and requires deep drainage to meet the agronomic requirements of cultivated plants (Oleszczuk *et al.*, 2008). Drainage depths of 0.4 to 0.6 m are typically required for productive grasslands, whereas drainage of approximately 1 m is generally assumed for arable production (Höper *et al.*, 2008).

⁷ Eddy covariance measurements of CO_2 fluxes are currently being made by this author and colleagues over cultivated peatlands in the Norfolk Fens (Morrison *et al.*, submitted.). At the current time, an annual estimate is unavailable.

Drainage and subsequent replacement of native (i.e. peat forming) vegetation with productive crops initiates sequential (often irreversible) changes to the physiochemical properties of peat soils (Zeitz & Velty, 2002; Oleszczuk *et al.*, 2008), large scale land subsidence (Hutchinson, 1980; Leifeld, Muller & Fuhrer, 2011; Dawson *et al.*, 2010; Figure 2.2), and an increase in radiative forcing due to altered GHG dynamics (Byrne *et al.*, 2004; Figure 2.1). In the absence of intervention (i.e. restoration), agricultural use of peatland is always associated with progressive (and ultimate) losses of peat from the landscape (Burton & Hodgson, 1987; Dawson *et al.*, 2010). Furthermore, peatland drainage has been a major cause of historical biodiversity loss (Couwenberg *et al.*, 2011).

Artificial lowering of peatland water tables initiates subsidence of the peatland surface (Dawson *et al.*, 2010; Leifeld, Muller & Fuhrer, 2011). Subsidence reflects a combination of: (i) primary consolidation; (ii) shrinkage; and (iii) biological oxidation (summarised in Table 2.4). Losses of peat via wind and water erosion (Warburton, 2003; Dawson & Smith, 2007), occasional fires (Holman, 2009) and small amounts of peat attached to (i.e. root) crops further contribute to surface lowering and net C losses (Gauci, 2008). The impact of subsidence is demonstrated at Holme Fen in the East Anglian Fens, where a fixed datum (Figure 2.2) has recorded approximately 4 m of peat wastage associated with drainage of surrounding peatland for agriculture since 1850 (Hutchinson, 1980). Furthermore, surface lowering increases the risk of flooding (Dawson *et al.*, 2010), and necessitates increasingly sophisticated drainage operations to maintain arable production and profitability (Morris *et al.*, 2010).

Table 2.4: Physical and biological processes contributing to subsidence in drained and cultivated peatlands.

Process	Description
Consolidation	Primary consolidation results from a loss of peat buoyancy and collapse of peat macropore structures due to the removal of supporting pore water after drainage (Dawson <i>et al.</i> , 2010). Consolidation may also be enhanced by the passage of agricultural traffic (Holman, 2009). Consolidation is purely physical and does not result in C loss, but serves to increase peat bulk (and C) density over time (Leifeld, Muller & Fuhrer, 2011). Consolidation dominates subsidence rates immediately following drainage but its importance declines over time (Leifeld, Muller & Fuhrer, 2011). Consolidation regains importance to overall subsidence rates each time the drainage base is lowered (Hutchinson, 1980; Leifeld, Muller & Fuhrer, 2011).
Shrinkage	Drainage and increased evaporative losses following drainage results in the shrinkage of peat soils (Dawson <i>et al.</i> , 2010). Similar to primary consolidation, shrinkage is purely physical and does not result in the release of C, but serves to increase peat bulk (and C) density over time (Leifeld, Muller & Fuhrer, 2011). The contribution of shrinkage to overall subsidence rates is greatest in the early stages of initial or repeat drainage (Dawson <i>et al.</i> , 2010). Initial subsidence rates of 180 mm yr ⁻¹ due to primary consolidation and shrinkage have been reported (Hutchinson, 1980, Holman, 2009).
Biological oxidation	Drainage alters redox conditions in the upper peat profile. Increased oxygen availability in the drained peat accelerates rates of biological oxidation (heterotrophic respiration). Rapid heterotrophic decomposition under oxic conditions results in large scale transfers of historically accumulated C to the atmosphere in the form of CO_2 (Couwenberg <i>et al.</i> , 2011) Estimates of the oxidative contribution to subsidence rates range from 28% to 100% (Grønlund <i>et al.</i> , 2008; Couwenberg <i>et al.</i> , 2010; Leifeld, Muller & Fuhrer, 2011). CO_2 losses are typically highest in the early stages of drainage, but decline over time due to the relative accumulation of recalcitrant over labile C fractions (Thompson, 2008; Leifeld, Steffens & Galego-Sala, 2012). Oxidative C losses dominate subsidence rates after the initial phase of consolidation and shrinkage (Dawson <i>et al.</i> , 2010). The ultimate disappearance of peat from a given location shows that oxidative losses must contribute 100% of observed subsidence rates during the final stages of peatland drainage (Page <i>et al.</i> , 2011). In the temperate zone, peat subsidence rates attributable to oxidation are often between 10 to 20 mm yr ⁻¹ , depending on peat type and drainage conditions (Hutchinson, 1980; Dawson <i>et al.</i> , 2010).
Other carbon losses	Additional losses of peat (and C) occur due to (i) wind borne losses; (ii) exports of dissolved and particulate organic C (Warburton, 2003; Couwenberg, 2011); and (iii) exports of C attached to (i.e. root) crops (Gauci, 2008). The fate of organic C transported by these processes in the wider environment remains poorly understood, but it is generally assumed that this C is ultimately respired to the atmosphere in the form of CO_2 (Lal, 2004). Occasional peat fires may result in additional peat loss and the release of C to the atmosphere (Holman, 2009).



Figure 2.2: The Holme Post at Holme Fen in the East Anglian Fenland. The post was installed in 1850 and has recorded over 4 m of peat wastage associated with four successive stages of drainage of surrounding farmland on peat soils (Hutchinson, 1980). A further consequence of the drainage is that Holme Fen currently supports the largest silver birch (*Betula pendula*) woodland in England. Image obtained by the author in December 2009.

The peatland CO_2 sink function is destroyed by drainage (Figure 2.1) as large volumes of previously saturated (i.e. stable) peat are rapidly decomposed on exposure to aerobic conditions (Höper *et al.*, 2008; Dawson *et al.*, 2010). Increased rates of heterotrophic respiration result in large-scale transfers of historically accumulated (i.e. old) soil C to the atmosphere as CO_2 (Kasimir-Klemedtsson *et al.*, 1997; Lohila *et al.*, 2004). CO_2 assimilation by productive crops can be effective in rendering drained peatlands a net *in situ* CO_2 sink during short periods, but labile crop residues remaining after harvest are generally ineffective in compensating for ongoing C losses (Lohila *et al.*, 2004; Shurpali *et al.*, 2009; Morrison *et al.*, submitted).

CH₄ emissions are usually negligible or negative following drainage due to increased rates of CH₄ oxidation (i.e. methanotrophy) (Maljanen *et al.*, 2004) but may remain high from drainage networks (Couwenberg, 2011; Carter *et al.*, 2012). N₂O emissions may be very high from drained peats due to enhanced mineralisation rates (Maljanen et al., 2004), that may be further exacerbated by additions of nitrogen (N) fertilizer to moist peat soils (Couwenberg, 2011). As the focus of this research is on CO₂, emissions/removals of CH₄ and N₂O are not further considered in this section.

National-scale GHG emissions from agricultural peatlands⁸ are reportable by parties to the Kyoto Protocol to the UNFCCC (Alm *et al.*, 2007; IPCC, 2006). In terms of CO₂, emissions factors (EFs) for agricultural peatlands in the temperate and boreal zones have been derived on the basis of peat subsidence rates (e.g. Berglund & Berglund, 2008; Leifeld, Muller & Fuhrer, 2011), modelling studies (e.g. Bradley., 1997) and direct flux (i.e. chamber and micrometeorological) measurements (e.g. Lohila *et al.*, 2004; Maljanen *et al.*, 2007; Grønlund *et al.*, 2008). Examples of available estimates of CO₂ EFs for cultivated boreal and temperate peatlands are summarised in Table 2.5. Direct (i.e. chamber or micrometeorological) annual CO₂ flux estimates are still lacking for temperate croplands on organic soils (Couwenberg, 2011), although an annual CO₂ balance will be available in June 2013.

⁸ GHG emissions from natural peatlands are not reported as these are considered to maintain the natural radiative balance of the atmosphere (i.e. considered as zero) (Alm *et al.*, 2007).

Mg CO ₂ -C ha ⁻¹ yr ⁻¹	Description	Reference
10±90%	Default EF for cultivated organic soils in the warm temperate region.	IPCC (2006)
5±90%	Default EF for cultivated organic soils in the cool temperate/boreal region	IPCC (2006)
0.79 to 7.5	Range of CO ₂ flux estimates measured using chambers and eddy covariance for Finnish grasslands on organic soils.	Maljanen <i>et al.</i> , (2007) and authors therein.
2.1 to 8.3	Range of CO ₂ flux estimates measured using chambers and eddy covariance for barley grown on organic soils in Finland.	Maljanen <i>et al.</i> , (2007) and authors therein.
1.09 to 12.5	Current UK EFs used to represent lowland peat drainage for peats less than and greater than 1 m in depth, respectively. Derived from peat subsidence rates and modelling (Bradley <i>et al.</i> , 1997).	Baggott et al., (2008)
3.2	Estimate of CO_2 losses derived on the basis of peat subsidence rates at the Holme Post (see Figure 2.2) in the East Anglian Fens. Assumes an average bulk density of 0.54 and a C content of 33%. A value of 32 Mg CO2-C was reported in the publication but represents a decimal error.	Gauci (2008)
3.5 to 5.2	Subsidence-based estimate of CO_2 loss for managed grassland on organic soils in Sweden. Assumes an oxidative fraction of 35%.	Berglund & Berglund, (2010)
5.2 to 7.9	Subsidence-based estimate of CO_2 loss for annual crops (excluding row crops) on organic soils in Sweden. Assumes an oxidative fraction of 35%.	Berglund & Berglund, (2010)
8.8 to 13	Subsidence-based estimate of CO_2 loss for row crops on organic soils in Sweden. Assumes an oxidative fraction of 35%.	Berglund & Berglund, (2010)
6 to 8	CO_2 losses estimated for drained and cultivated organic soils in Norway. Estimates based on chamber-based CO_2 flux measurements, peat subsidence rates and changes in ash content.	Grønlund et al. (2008)
2.5 to 5.5	Subsidence-based estimate of CO_2 loss for drained temperate fens in Switzerland. Assumes an oxidative fraction of 28to 64%.	Leifeld, Muller & Fuhrer, (2011)

Table 2.5: Examples of CO₂ emissions factors (EFs) for cultivated lowland peatlands in the temperate and boreal zones.

 CO_2 loss rates from cultivated peatlands vary (Table 2.5) but can be amongst the highest from any type of land use (Lohila *et al.*, 2004; Couwenberg *et al.*, 2011). As well as methodological differences⁹ (Table 2.5), differences in CO_2 EFs relate to: (i) climate (ii) peat type (i.e. peat chemistry); (iii) drainage depths; (iv) cultivation intensity (i.e. tillage intensity, fertilisation, liming); (v) crop types and management intensity (CO_2 losses increase in the order: permanent grassland, cereals to row crops); and (vi) time since drainage commenced (Kasimir-Klemedtsson *et al.*, 1997; Byrne *et al.*, 2004; Berglund & Berglund, 2008; Höper *et al.*, 2008; Dawson *et al.*, 2010; Leifeld, Muller & Fuhrer, 2011).

In the UK, CO_2 emissions are currently reported for 150,000 ha of drained and cultivated lowland fen peatland, of which 145,000 ha is in East Anglia (Thompson, 2008; Choudrie *et al.*, 2009). Current UK CO₂ emissions factors (EFs) were derived on the basis of subsidence rates and the Century model (Bradley, 1997), estimating CO₂ losses at 12.8 Mg CO₂-C ha⁻² yr⁻¹ (1280 g CO₂-C m⁻² yr⁻¹) for peats depths greater than 1 m, and 1.09 Mg CO₂-C ha⁻² yr⁻¹ (109 g CO₂-C m⁻² yr⁻¹) for shallower peats (i.e. those that have been degraded under arable land use). The difference is attributed to losses of easily decomposable (i.e. labile) C with time since drainage (Bradley, 1997; Baggot *et al.*, 2008).

At national scale, application of UK EFs to the area of cultivated fenland¹⁰ results in combined gaseous CO_2 emissions of 1.66 Mt CO_2 m⁻² yr⁻¹ (Baggott *et al.*, 2008;

⁹ Estimates based on peat subsidence rates represent a measure of total C loss from peat soils over time (i.e. including losses via aeolian, fluvial and other processes) and should more correctly be reported in units of CO_2 equivalents (CO_2 -eq).

¹⁰ Assuming 240 and 1260 km² of deep (>1m) and shallow peat (<1m), respectively (Bradley, 1997; Thompson, 2008).

Thompson, 2008). Total CO₂ losses from cultivated UK fens are actually reported at $1.15 \text{ Mg CO}_2 \text{ yr}^{-1}$, as it is assumed that a fraction of the C is not emitted in the form of CO₂, although it is unclear how this reduction was calculated (Thompson, 2008). More recent analyses indicate the area of shallow fen peat may have been underestimated (i.e. Table 2.2), and total CO₂ (and N₂O) emissions could be much higher (Thompson, 2008, Natural England, 2010). These large and ongoing CO₂ emissions demonstrate significant (technical) mitigation potential, should improved land management (i.e. restoration) prove effective in reducing/reversing net CO₂ losses.

In the absence of more comprehensive (i.e. flux) data for the UK, the CO₂ EFs reported in the NIR (see Table 2.5) remain the best currently available estimates of CO₂ losses for arable fens. The accuracy of these estimates is questionable, as they are static and do not reflect any variability resulting from peat conditions (other than a broad consideration of peat depth) or agricultural management practices. However, these values were used as the basis for recent assessments aiming to quantify the magnitude of CO₂ losses from arable fens, as well as first-order analyses of net GHG reductions resulting from restoration activity (e.g. Natural England, 2010; Morris *et al.*, 2010; Worrall *et al.*, 2011). As such, these values form the baseline for estimating any annual CO₂ emissions reductions in this thesis (the limitations of this are discussed in Chapter 8). The higher value (320 g CO₂-C m⁻² yr⁻¹) of Gauci (2008) is also used as a means of better constraining the (potential) uncertainty range.

2.6 Landscape scale fenland restoration

The restoration of agriculturally degraded fens is expected to become an increasingly important land management activity over coming decades (Grønlund *et al.*, 2008;

Couwenberg *et al.*, 2011). This reflects declining agricultural productivity (and profitability) with decreasing peat depth (Morris *et al.*, 2010) coupled with wider concerns over biodiversity conservation and ecosystem service provision (Hughes *et al.*, 2011). Ecological theory shows restoration success¹¹ scales positively with size (Moreno-Mateos et al., 2012) and a number of landscape-scale fen restoration projects are now underway in the UK (Friday & Colston, 1999; The National Trust, 2007; The Great Fen Project, 2012), continental Europe (Couwenberg *et al.*, 2011) and elsewhere.

Peatland restoration schemes have the potential to positively influence (i.e. reduce) overall GHG emissions compared with productive land uses (Wilson *et al.*, 2008; Couwenberg *et al.*, 2011). Consequently, large-scale peatland rehabilitation projects are generating strong interest from land managers, scientists and policy-makers concerned with identifying and exploiting land-based options with the potential to reduce GHG emissions and mitigate anthropogenic climate change (Thompson, 2008; Baird, Holden & Chapman, 2009; Morris *et al.*, 2010; Birkin *et al.*, 2011).

In terms of C-orientated management¹², the objective of peatland restoration is to bring back conditions for active peat formation and net C accretion (Tuittila *et al.*, 2004; Herbst *et al.*, 2012). In theory, degraded fens can be restored to C accumulating systems, provided abiotic and biotic conditions can be successfully manipulated (Hendricks *et al.*, 2007; Herbst *et al.*, 2012). Restoration practices differ, depending on the specifics of a given location, but generally involve some form of hydrological

¹¹ Success can only be defined relative to the goals of a given restoration project, which may or may not explicitly include net C sequestration or GHG emissions reductions.

¹² Historically, C orientated land management has not typically been the main driver for peatland restoration, but is becoming increasingly recognised as an important aspect of many restoration schemes, due to the unique ability of peatlands to store and/or sequester C.

manipulation ('rewetting') to promote the abiotic conditions required for succession towards a characteristic (i.e. peat-forming) flora (Baird, Holden & Chapman, 2009; Haapalehto *et al.*, 2011).

In terms of fenland restoration, rewetting requires diversion of minerotrophic waters of suitable quantity and quality from a wider catchment (Tuittila *et al.*, 2004). Such requirements may be hampered by allocation rights (Chimner & Cooper, 2003a) and/or altered peat and hydrological conditions at site and/or catchment scale (Holden, Chapman & Labadz, 2004; Haapalehto *et al.*, 2011). The speed and trajectory of revegetation will depend on site (i.e. starting conditions) conditions together with propagule availability (i.e. presence/absence of a viable seed bank and/or distance from potential colonists) (Stroh et al., 2012; Hughes *et al.*, 2011), and may require some form of assisted recovery (Patzelt, Wild & Pfadenhauer, 2001). In general, restoration success will be influenced by starting conditions (i.e. peat condition, ecological factors), the ability to successfully regulate water levels, and time under restoration management (Höper *et al.*, 2008).

Rewetting of arable fens is expected to a lead to shift from rapid aerobic to slow anaerobic decomposition (Baird, Holden & Chapman, 2009). Together with renewed CO_2 uptake following revegetation, restoration is expected to reduce or reverse net losses of CO_2 (Worrall *et al.*, 2011), increase CH_4 emissions (Wilson *et al.*, 2008; Baird, Holden & Chapman, 2009; Levy et al., 2012), with uncertain responses expected from N₂O (Hendricks et al., 2007; Höper *et al.*, 2008). Despite this, it is generally assumed that fenland rehabilitation will deliver net GHG benefits (i.e. a reduced global warming potential) compared to arable land use, mainly due to the scale of avoided CO_2 loss and/or renewed CO_2 sequestration (Thompson, 2008; Natural England, 2010; Couwenberg, 2011). Within this framework, Worrall *et al.* (2011) suggested the benefits of peatland restoration could be threefold, potentially resulting in: (i) a net reduction in CO_2 emissions relative to the previous land use (i.e. an avoided CO_2 loss); (ii) a transient C sink (i.e. during revegetation); and (iii) (re-)establishment of a nearperpetual (or at least long-term) C sink characteristic of pristine (or relatively intact) peatland environments.

Peatland restoration is of increasing relevance to national and international climate policy. As a party to Kyoto Protocol of the UNFCCC, the UK is required to reduce GHG emissions to five percent of 1990 levels during the first commitment period (2008 to 2012). UK domestic targets require that emissions are further reduced to 80% of 1990 levels by 2050 (Climate Change Act, 2008). Under IPCC (2006) guidance, GHG emissions/removals from managed peatlands are reported using a three-tier methodology (IPCC, 2006; Table 2.6). Countries are encouraged to develop Tier 2 and 3 reporting methods whenever practicable (IPCC, 2006; Couwenberg, 2011).

Tier	Description
1	Uses default emissions factors (IPCC, 2006) that are multiplied by the area of a reportable land use activity (e.g. IPCC (2006) values in Table 2.5).
2	Utilise location-specific (i.e. regional or national) emissions factors derived from empirical measurements, such as direct flux data or changes in soil C (i.e. UK values in Table 2.5).
3	Utilise dynamic emissions factors derived on the basis of process-based models (i.e. using meteorological inputs).

 Table 2.6: Summary of the three tiers used in national greenhouse gas inventories

At the current time (2012), emissions reductions resulting from peatland restoration are not explicitly included under article 3.4 of the Kyoto agreement (Natural England, 2010). As of COP17¹³, however, 'Wetland Drainage and Rewetting' can be included in national reporting on a voluntary basis (Bain, 2012; Bain et al., 2012). It is unclear whether the UK will adopt this category (Bain, 2012; Bain et al., 2012). Despite this, parallel interest exists for inclusion of peatland restoration schemes within voluntary C markets (Thompson, 2008; Natural England, 2010). Either way, regionally-specific EFs are required that can be used to quantify the net GHG benefits resulting from restoration.

In terms of land C accounting, EFs must be robust, in that they are measurable, reportable and verifiable (Joosten & Couwenberg, 2009). Ideally, (Tier 2) EFs are developed from multiple sites over five year (or longer) periods to characterise the spatial and interannual variability in GHG exchanges (Thompson, 2008; Joosten & Couwenberg, 2009). In the UK, a considerable research agenda is now underway to develop (Tier 2) EFs for lowland peatlands, and build the evidence base for inclusion of peatlands in national GHG reporting (Birkin *et al.*, 2011; Evans *et al.*, 2011; Worrall *et al.*, 2011), although such research efforts remain in the preliminary stages.

A limited number of studies have reported first-order estimates of net GHG emissions benefits of arable fenland rehabilitation in the UK (Table 2.7). In all cases, such assessments assume reduced heterotrophic CO_2 loss and development of a CO_2 fixing plant cover result in net removals of CO_2 from the atmosphere at a rate similar to undamaged (or at least semi-natural) peatlands (in some cases using EFs from

¹³ Conference of Parties to the United Nations Framework Convention on Climate Change held in Durban during December 2011.

undamaged bogs), typically after some (variable) period characterised by transitional CO_2 (and non- CO_2 GHG) dynamics (Table 2.7). Such assessments are currently constrained by (very) limited data on CO_2 (and other GHG) fluxes from restored exarable fens (Byrne *et al.*, 2004; Höper *et al.*, 2008; Baird, Holden & Chapman, 2009) and uncertainty as to when (or even if) restored ex-arable fens will become a net sink for atmospheric CO_2 . Moreover, UK assessments have often been based on data from continental Europe (discussed below), and are further hampered by the paucity of (baseline) data on CO_2 emissions from arable (discussed above) and undamaged reference sites (Baird, Holden & Chapman, 2009).

Table 2.7: Summary and description of studies aiming to quantify greenhouse gas benefits of fenland restoration in the United Kingdom.

Reference	Description
Gauci (2008)	Study aiming to quantify the GHG benefits of the Great Fen project area in East Anglia. Estimated CO_2 losses from agricultural land use on the basis of subsidence rates and peat characteristics (Table 2.5). Applied available literature values of GHG fluxes to restored fens and wet grasslands for three phases described by Joosten & Augustin (2006) using three scenarios over a 100 year timescale (Scenario 1: 5 years at phase 1; 15 years at phase 2 and 80 years at phase 3. Scenario 2: 20 years at phase 1; 20 years at phase 2 and 65 years at phase 3. Scenario 3: 50 years at phase 1; 1 year at phase 2 and 49 years at phase 3. Assumed CO_2 emissions from wet grasslands at -109.86, -109.86 and -100 g CO_2 -C m ⁻² yr ⁻¹ , and for fens at -54.5, -221.99 and -100 g CO_2 -C m ⁻² yr ⁻¹ for phases 1, 2 and 3, correspondingly (values from Dawson & Smith, 2007, units converted). On the basis of scenario 2, estimated a net (GHG) offset potential of -23 g CO_2 -e m ⁻² yr ⁻¹ compared to continued arable land use.
Natural England (2010)	Review of peatland area and C storage in England. Estimated net GHG emissions reductions on the basis of available emissions estimates. First study to provide annual EFs for UK peatlands. EFs for fens based on data from the UK (Bradley, 1997), Central Europe (Couwenberg et al., 2008) and Tier 1 IPCC (2006) N ₂ O values. For fens, provides EFs of 26.17 Mg CO ₂ -e ha ⁻¹ yr ⁻¹ for deep cultivated (>0.4 m) peats; 4.58 Mg CO ₂ -e ha ⁻¹ yr ⁻¹ for undamaged and restored fens. CO ₂ emissions estimated using: 109 g CO ₂ -C m ⁻² yr ⁻¹ for cultivated wasted fens (Bradley, 1997); 611 g CO ₂ -C m ⁻² yr ⁻¹ for deep cultivated fens (modelled values derived from Couwenberg et al. (2008) assuming a drainage depth of -60 cm); and -97 g CO ₂ -C m ⁻² yr ⁻¹ for undamaged and restored fens (modelled values derived from Couwenberg et al. (2008) assuming water levels are maintained at a depth of -5 cm). Estimated hypothetical net GHG emissions reductions of 1.14 and 0.07 Mt CO ₂ -e if all areas of degraded deep (>0.4 m) and wasted (<0.4 m) fen peatland was brought under restoration management, respectively. Calculations applied on a 40 year basis, assuming 10 years of restoration emissions, and thirty years of emissions characteristic of undamaged fens (although note that values for restoration and undamaged fens are the same).
Morris <i>et al</i> . (2010)	Study exploring the impacts of peatland restoration on food production and security. Estimated the economic benefits of peatland restoration in four target peatland restoration areas (The East Anglian Fens, The Humberhead Levels, The Somerset Moors and Levels, and The Lyth Valley in Cumbria). For GHG emissions, applied EFs from Natural England (2010 – above). Assumed fully restored peatlands (of all types) would result in net CO_2 -e removals from the atmosphere using the Natural England (2010) EF for undamaged raised bogs (-4.11 Mg CO ₂ -e ha ⁻¹ yr ⁻¹ , which includes a net removal of -146 g CO ₂ -C m ⁻² yr ⁻¹). A footnote notes that restored lowland fens may not be suitable for this level of peat formation and could continue to show positive emissions.

Evidence from a limited number of European fens¹⁴ shows restoration (or less intensive) land management can result in (re-)creation of net CO₂ sinks after relatively short (i.e. decadal) periods (e.g. Hendricks *et al.*, 2007; Veenendaal *et al.*, 2007; Herbst *et al.*, 2012). Such results were obtained at sites that were restored following less intensive (i.e. gazing meadows) and/or shorter periods of agricultural management than typical of the UK (i.e. East Anglian) context. These results cannot simply be extrapolated to UK conditions (and the Fenland in particular) due to differences in climate, peat condition resulting from historical land use activity (i.e. time since drainage, tillage intensity, etc.) and other ecological and landscape factors (i.e. water allocation rights).

Conversely, results from other types of restored peatland have shown that restoring high water levels and revegetation do not necessarily result in C dynamics characteristic of undamaged peatland environments (i.e. assuming undamaged sites are net CO_2 sinks), at least in the near-term (e.g. Samaritani *et al.*, 2011). Furthermore, contemporary landscapes and climates differ substantially from conditions under which peatlands developed (Holden, Chapman & Labadz, 2004; Hughes *et al.*, 2011). As such, it remains uncertain whether restored fens will show converging or diverging successional trends relative to pre-disturbance analogues (Moreno-Mateos *et al.*, 2012).

2.7 Peatland management and environmental change

Future peatland management and restoration activity will take place against the background of anthropogenic climate change (Friedlingstein & Solomon, 2005; Hughes *et al.*, 2011). In a wider context, the spatial and temporal evolution of terrestrial C sinks

¹⁴ A summary of available annual CO_2 emissions estimates is presented in Table 8.1 for comparison with the annual CO_2 balance estimated in this thesis.

and sources remains one of the largest uncertainties for predictions of future climate dynamics (Cox *et al.*, 2000; Heimann & Reichstein, 2008; Canadell *et al.*, 2010). This is of particular concern with respect to peatlands due to the large amounts of C stored as peat, and its potential release in response to climatic variation and change (Sottocornola & Kiely, 2010).

In terms of NEE, peatland responses to climatic variation or change will depend on whether GPP and ER are differentially or similarly affected (Cai *et al.*, 2010; Sulman *et al.*, 2009; 2010; Flanagan & Syed, 2011). Current consensus suggests CO₂ fertilisation, higher temperatures and extended growth seasons (i.e. in spring and autumn) will enhance ecosystem production (Heimann & Reichstein, 2008; Cai *et al.* 2010), although such responses are expected to saturate due to nutrient constraints (Heimann & Reichstein, 2008). At the same time, warmer conditions, changing precipitation patterns and associated changes in peatland water balance (i.e. lower water levels and/or soil moisture) are expected to accelerate CO₂ losses, potentially outweighing some or all of benefits resulting from enhanced GPP (Gorham, 1991; Rounsevell & Reay, 2009; Cai *et al.*, 2010).

In contrast, studies at boreal fens have shown similar responses from GPP and ER in response to warmer and/or drier conditions. Sulman *et al.* (2010) and Flanagan *et al.* (2011), for example, showed NEE effectively remained balanced by responses of similar (but opposing) magnitude from GPP and ER under drier and/or warmer conditions, respectively. Furthermore, it is unclear how CO_2 exchange will respond to an increasing frequency of meteorological extremes (i.e. increased drought frequency, more intense precipitation events), which could have a larger (and potentially longer-

term) impact on ecosystem functioning than changes in average conditions alone (Ciais *et al.*, 2005; Reichstein *et al.*, 2007; Heimann & Reichstein, 2008; Rogiers *et al.*, 2008).

Field studies obtained under contemporary environmental conditions can provide important insights into potential ecosystem responses to environmental variability and change (Glen *et al.*, 2006; Cai *et al.*, 2010). In managed and/or restored fens, such information is required to identify land management interventions (i.e. hydrological regulation) that could prove effective in maintaining/enhancing peatland soil C stocks (and habitats) into the future, at least in the near-term.

2.8 Summary

This chapter has provided a review of the scientific and policy literature relevant to this research. The importance of peatlands in terms of terrestrial C storage was highlighted. The physical and biological processes operating in intact and agriculturally degraded peatlands were described. The current state of knowledge pertaining to lowland fen rehabilitation was discussed, as well as the (potential) relevance of restoration to national and international policy frameworks. The importance of understanding potential ecosystem responses to environmental change in terms of improved peatland management was highlighted.

At the current time, very little data pertaining to CO_2 (and other non- CO_2 GHG) fluxes from managed and restored lowland fens exist for the UK. Estimates from Bradley (1997) and Gauci (2008) represent the current best estimates of CO_2 losses from arable fens in East Anglia. Understanding the current and potential future role of lowland fens in terms of the UK land C budget requires quantification of all climate-relevant C and GHG fluxes across a range of site types, together with their spatial and temporal variability. Moreover, improved knowledge of the spatial and temporal dynamics and drivers of land/atmosphere GHG exchanges is important for effective management of semi-natural and managed peatlands and their C (and GHG) balances in a changing environment.

In this context, field measurements of NEE at ecosystem scale represent a first step towards full C and GHG accounting. Measurements are required to: (i) assess the current role of managed lowland fens within the UK land C budget (i.e. developing EFs); (ii) gain knowledge of the processes and controls driving land/atmosphere CO_2 exchange and how these might be manipulated for increased (decreased) CO_2 uptake (loss); and (iii) provide insight into the potential responses of ecosystem CO_2 balances to projected climatic variability and change. This research therefore represents an important first step towards filling these important gaps in data and knowledge.

Chapter three: Assessing ecosystem-scale CO₂ budgets: eddy covariance

This chapter presents an overview of the main tool used in this research: the micrometeorological eddy covariance (EC) technique. A description of the theory and practical application of EC is provided. Details of the post-processing and quality control procedures required to obtain reliable flux estimates are outlined. Methods used to fill unavoidable gaps in EC flux records, and to partition measurements of NEE into estimates of GPP and ER are described. The reconstruction of the surface energy balance closure as a means of assessing the plausibility of EC flux datasets is discussed. A short description of the main uncertainties influencing time-integrated estimates of NEE is provided.

3.1 Eddy covariance: overview and measurement principle

EC is considered the most defensible method of assessing ecosystem-scale energy and trace gas budgets (Baldocchi *et al.*, 2001; Laine *et al.*, 2006). As such, EC is deployed at over 500 sites, globally, within the framework of the FLUXNET (2012) initiative. Widespread adoption of EC reflects: (i) an ability to measure water, energy and trace gas fluxes (mainly CO_2 but increasingly CH_4 and N_2O) on a (quasi-)continuous and long-term basis; (ii) a measurement scale of direct relevance to whole ecosystem flux dynamics; and (iii) the absence of any significant measurement artefact (Baldocchi, 2003).

An increasing number of EC studies have focused on CO_2 fluxes at peatland environments; however, these have primarily focused on near-pristine peatlands of the arctic and boreal regions (e.g. Roulet *et al.*, 2007; Nilsson *et al.*, 2008; Lund *et al.* 2010). Managed peatlands of temperate (and tropical) climates remain strongly underrepresented (Couwenberg, 2011; Teh *et al.*, 2011).

EC is based on sensing the turbulent motion of the atmospheric surface layer¹⁵ and the concentration of an atmospheric scalar of interest (in this case CO₂). Atmospheric turbulence is driven by mechanical (shear) and thermal (convective) forces, which generate eddies of various frequencies (Stull, 1988). These turbulent eddies represent the primary mode of vertical transport in the surface layer, where vertical variation in turbulent transport is independent of height (Stull, 1988; Foken *et al.*, 2012). Measurements obtained using EC systems installed at a fixed height (z_m) on a flux tower (Figure 3.1) are therefore representative of fluxes across the land/atmosphere interface (Stull, 1988). Furthermore, turbulence acts as a physical averaging operator (Moncrieff *et al.*, 2004), so measurements are representative of vertical exchanges averaged over a large downwind area (hectares to km²) or 'flux footprint' (Baldocchi, 2003).

The practical application of EC combines fast response sonic anemometerthermometers (SATs) and infrared gas analysers (IRGAs) (Figure 3.1). Differences in EC applications relate to whether open or closed-path IRGAs are deployed (Massman, 2004; Haslwanter, Hammerle & Wohlfahrt, 2009; Munger, Loescher & Luo, 2012). Open-path IRGAs are used in this research, and discussion focuses on measurements with this sensor type (Figure 3.1).

¹⁵ The atmospheric surface layer is the lower 20 to 50 m of the atmospheric boundary layer (Stull, 1988; Foken *et al.*, 2012).



Figure 3.1: Eddy covariance instrumentation. The image shows a CSAT3 sonic anemometer and a LI-COR Li7500 open-path H_2O/CO_2 analyser. Image obtained by the author at the Bakers Fen study site in February 2010.

High frequency (10 to 20 Hz) measurements are required to resolve the full range of flux-transporting (high frequency) turbulent motion (Foken, 2008). Simultaneous fluctuations in the vertical wind speed (*w*) and scalar (i.e. CO_2) concentrations (*c*) are obtained using Reynolds averaging (Baldocchi, 2003). Surface/atmosphere exchanges are computed as the mean covariance between turbulent fluctuations in these variables (Burba & Anderson, 2012). Averaging intervals of thirty minutes are typically used, reflecting a balance between requirements for capturing low frequency turbulent motion (Moncrieff *et al.*, 2004), and the resolution of the diurnal cycle. Land/atmosphere fluxes (*F_c*) are computed using:

$$Fc = \overline{w'c'} = \frac{1}{N-1} \sum_{i=0}^{N-1} (w - \overline{w})(c - \overline{c})$$
 3.1

(Foken, 2008), where *w* is vertical wind speed (m s⁻¹); *c* is the atmospheric mixing ratio (mol mol⁻¹); N is the number of high frequency measurements (i.e. 36000 for a thirty minute averaging interval); primes denote instantaneous deviations from the 30 minute mean; and overbars represent (i.e. thirty minute) averages. Similar calculations are used for sensible and latent heat fluxes¹⁶ (and other atmospheric scalars). In practice, scalar sensors (i.e. IRGAs) do not measure atmospheric mixing ratios (Baldocchi, 2003). Fluxes are computed using the Webb, Pearman & Leuning (1980) algorithm to account for density changes driven by temperature and humidity fluctuations (Table 3.1).

3.2 Theoretical assumptions and data post-processing

The successful application of EC requires that a number of theoretical assumptions are met. The most important of these are: (i) that sensors can respond to high frequency variations in atmospheric turbulence and scalar concentrations (Moore, 1986; Munger, Loescher & Luo, 2012); (ii) measurements are made within the surface (constant flux) layer (Mahli, McNaughton & Von Randow, 2004); (iii) a flat homogeneous surface (or fetch) with a uniform source/sink status exists for an extended upwind distance from the tower (Horst & Weil, 1993; Foken, 2008); (iv) absence of horizontal advection (Leuning, 2004); (iv) fluctuations average to zero over time (Baldocchi, 2003; Foken, 2008); (v) turbulent exchange is stationary (e.g. steady-state) and fully developed (Foken & Wichura, 1996; Foken *et al.*, 2004; 2012); (vi) atmospheric density

¹⁶ Sensible heat (H) and latent heat (LE) fluxes are converted to energy units (W m-2) by multiplication by the specific heat of air (ρCP) and the latent heat of evaporation (λ), respectively (Burba & Anderson, 2012).

fluctuations are negligible (Webb, Pearman & Leuning, 1980; Burba & Anderson, 2012); (vii) measured fluxes originate from the surface of interest (Scheupp *et al.*, 1990; Burba & Anderson, 2012).

The theoretical assumptions of the EC technique are rarely (if ever) fully met in practice (Moncrieff *et al.*, 2004; Ruppert *et al.*, 2006). As such, appropriate site selection and tower placement, together with a number of post-processing and data quality control (QC) procedures are required to obtain reliable flux estimates (Rebmann *et al.*, 2012). Typical data post-processing routines involve (see Table 3.1): (i) removal of spikes and physically implausible values in raw (20 Hz) EC data (Vickers & Mahrt, 1997); (ii) removal of lags between SAT and scalar sensors (Foken, 2008); (iii) rotation of SAT coordinate systems (Wilczak *et al.*, 2001; Lee, Finnegan & Paw U, 2004;); (iv) conversion of SAT sonic-temperature measurements to air temperature fluctuations (Schotanus *et al.*, 1983); (v) calculation of sensible and latent heat flux coefficients (Mauder *et al.*, 2008); (vi) corrections for high frequency co-spectral¹⁷ losses (Moore, 1986); (vii) adjustment of concentration measurements related to temperature and humidity fluctuations (Webb, Pearman & Leuning, 1980); and (viii) corrections for CO₂ storage in the air column below *z_m* (Papale *et al.*, 2006).

¹⁷ The cross- or co-spectra represents the distribution of the covariance between the vertical wind speed and a scalar expressed as a function of the frequency of turbulent motion. The co-spectral distribution describes how much flux is transported at each frequency within the measured frequency range.

Table 3.1: Summary and description of post-processing procedures for the calculation of fluxes using the eddy covariance technique

Post-processing procedure	Description and reason for application
Spike removal	Applied to remove spikes and non-physical values in raw EC measurements due to instrument and electrical noise (Vickers & Mahrt, 1997; Rebmann <i>et al.</i> , 2012). Values identified as spikes are either removed (shortening the time series) or replaced by linear interpolation (Mauder & Foken, 2004).
Physical consistency tests	Applied to remove values that fall beyond realistic consistently limits (Mauder & Foken, 2004). Similar to spikes, non-physical values may relate to electrical noise or physical interference in SAT or IRGA sensing volumes (i.e. water accumulation on sensors). Non-physical data are excluded from any further flux computations.
Angle of attack dependent correction	Applied to omni-directional SATs to correct for imperfect cosine response due to self-shading of transducers by sensor head mountings (Gash & Dolman, 2003; Munger, Loescher & Luo, 2012).
Sensor lag removal	Applied to remove lags between sonic anemometer and scalar sensors due to spatial separation and align raw EC measurements in time. Performed using cross-correlation to maximise the covariance between SAT measurements of the vertical wind speed and scalar sensors (Foken, 2008).
Coordinate rotation	Applied to SAT data to align sensors with the local terrain and to remove contamination of the vertical wind vector by the horizontal components of atmospheric turbulence (Burba & Anderson, 2012). Can be applied by rotating coordinates during each flux averaging interval or over longer time intervals. The planar fit method is currently the recommended approach where the vertical flux is calculated perpendicular to a plane determined from SAT turbulence measurements over days to months (Wilczak <i>et al.</i> , 2001; Burba & Anderson, 2012).
Conversion of sonic temperature to true temperature	Speed-of-sound measurements of SATs provide a measure of sonic temperature which is <i>circa</i> 1% to 2% higher than true air temperature due to air density (i.e. related to humidity, pressure and temperature) effects (Rebmann <i>et al.</i> , 2012). The sonic-temperature is converted to measurements of true temperature for calculation of the sensible heat flux (Schotanus <i>et al.</i> , 1983).

Post-processing procedure	Description and reason for application
Calculation of sensible and latent heat flux coefficients	Covariances between the vertical wind speed and water vapour and temperature fluctuations must be multiplied by the latent heat of evaporation and a sensible heat flux coefficient to obtain energy fluxes in W m ⁻² . Coefficients are calculated for each thirty minute period to account for dependencies on temperature and humidity (Mauder <i>et al.</i> , 2008).
Frequency response corrections	Limitations in the geometry and time constants of EC systems result in the loss of high frequency flux contributions (Baldocchi, 2003). High frequency spectral losses are greatest during stable atmospheric conditions and lowest during strongly convective conditions (Baldocchi, 2003). Frequency response corrections are applied to all H, LE and CO ₂) fluxes. Corrections are typically applied by correcting measured co-spectra to idealised spectral models using the transfer function approach of Moore (1986). The use of finite (i.e. thirty minute averaging intervals also results in the loss of low frequency flux contributions; however, low frequency losses decrease as measurement height declines and are typically not corrected for in EC applications over low vegetation (Massman & Clement, 2004; Foken, 2008).
Adjustment for atmospheric density fluctuations	Infrared gas analysers do not measure atmospheric mixing ratios (i.e. moles per mole of dry air) of water vapour or CO_2 but the absolute/molar density (i.e. g m ⁻³ or mol m ⁻³) of these quantities (Baldocchi, 2003; Leuning, 2004). Absolute/molar density measurements are influenced by fluctuations in temperature and humidity. The Webb, Pearman and Leuning (1980) procedure is applied to LE and NEE fluxes to adjust for changes in concentration measurements that are related to density fluctuations and not changes in trace gas concentration.
CO ₂ storage correction	During periods of low turbulent mixing CO_2 may accumulate at the surface and not reach the measurement height. The storage term is estimated from profile measurements (if available) or successive IRGA concentration measurements made at the measurement height. CO_2 concentration measurements and added to the turbulent exchange of CO_2 . The storage term is applied before QC to avoid double-counting of CO_2 (Papale <i>et al.</i> , 2006; Aubinet <i>et al.</i> , 2012).

Table 3.1 (continued): Summary and description of post-processing procedures for the calculation of fluxes using the eddy covariance technique

3.3 Quality control

Quality control (QC) is an important aspect of the EC method and is required to identify and exclude data of suspect quality¹⁸. QC procedures applied to (i.e. thirty minute) flux estimates are site-specific (Foken *et al.*, 2004) but typically include (Table 3.2): (i) removal of fluxes when a significant fraction of data are removed prior to flux computations, such as when IRGA and SAT measurements become unreliable during precipitation (i.e. rainfall, frost) events (Foken *et al.*, 2004; Ruppert *et al.*, 2006; Foken, 2008); (ii) rejection of statistical outliers in flux (i.e. NEE) time series (Papale *et al.*, 2006; Elbers *et al.*, 2011); (iii) statistical tests for steady-state conditions and developed turbulence (Foken *et al.*, 2004 2012; Ruppert *et al.*, 2006; Papale *et al.*, 2006); (iv) footprint modelling to assess the spatial context of flux measurements (Scheupp *et al.*, 1990; Kormann & Meixner, 2003; Rannik *et al.*, 2012).

¹⁸ I.e. non-physical values or measurements that violate the theoretical assumption of the eddy covariance technique

Table 3.2: Summary of procedures used in the quality control eddy covariance flux measurements

Quality control procedure	Description and reason for application
Raw data removal	Fluxes are typically rejected when spike removal and/or physical consistency limits result in more than 1% of raw data removal prior to flux computations (Foken, 2008).
Outlier detection	Applied to identify statistical outliers and clearly non-physical values. Outliers are typically identified using the median absolute variation approach (Papale <i>et al.</i> , 2006). Day- and night-time measurements treated independently using a moving window. Care must be taken to avoid the removal of physical fluxes (Elbers <i>et al.</i> , 2011).
Stationarity test	Used to reject data obtained during non-steady state (i.e. time-varying) conditions. Applied by comparing the covariance calculated for thirty minute periods with the covariance calculated during approximately six shorter (i.e. five minute) subsets of the same thirty minute period (Foken <i>et al.</i> 2003; 2012; Ruppert <i>et al.</i> 2006).
Integral turbulence test	Statistical tests for fully developed and unperturbed turbulence. Integral turbulence statistics are calculated as the ratio between the standard deviation of the vertical wind speed and the friction velocity (u^*) . Integral turbulence statistics are compared to modelled values parameterised for different stability ranges (Foken <i>et al.</i> 2003; 2012; Ruppert <i>et al.</i> 2006).
<i>u</i> * test	CO_2 flux measurements are challenging during nocturnal periods due to the development of stable atmospheric conditions. The friction velocity (u^*) provides a measure of the shear stress exerted by the atmosphere at the surface. CO_2 flux measurements typically become more variable at low u^* values. The u^* test is used as a means of identify measurements obtained during periods of low turbulent mixing.
Footprint	The flux footprint defines the area 'seen' by the flux tower. The size of the footprint depends on measurement height, surface roughness (i.e. vegetation height), and wind direction and atmospheric stability (Burba & Anderson, 2012). Flux footprints become largest during strongly stable atmospheric conditions (i.e. at night). Footprint models (e.g. Scheupp <i>et al.</i> , 1990; Kormann & Meixner, 2003) are used to estimate the size of the downwind area and peak location contributing to measured fluxes.
3.3.1 Nocturnal flux measurements

One of the most significant challenges for EC (CO₂) flux measurements relates to nocturnal periods (Aubinet *et al.*, 2012). Under thermally stable conditions (i.e. calm summer nights), respired CO₂ may accumulate below z_m (Papale *et al.*, 2006; Aubinet *et al.*, 2000; 2012). In the worst case, horizontal advection may transport CO₂ away from the site of production, resulting in underestimation of nocturnal NEE and overestimation of the CO₂ sink strength (Goulden *et al.*, 1996; Aubinet *et al.*, 2012). This issue is addressed by rejecting fluxes obtained during periods of stable stratification, typically using a friction velocity (*u**) threshold (Goulden *et al.*, 1996; Papale *et al.*, 2006; Lohila *et al.*, 2011; Aubinet *et al.*, 2012). Papale *et al.* (2006), for example, reported annual NEE became less negative when high *u** values were used to filter data. Missing data are replaced with values derived from measurements obtained under fully turbulent conditions (discussed below).

3.4 Data gap-filling

Gaps in EC flux datasets are unavoidable and occur due to system downtime (i.e. instrument or system power failures) and QC procedures (Papale, 2012). Data coverage at EC sites is typically 40 to 60% at annual timescales (Falge *et al.*, 2001), although 40% coverage is considered adequate for obtaining defensible annual sums (Falge *et al.*, 2001; Rogiers *et al.*, 2009). Nocturnal data coverage is generally lower than during the day for reasons discussed above. Data gaps are unproblematic for analyses of functional relationships (i.e. light or temperature responses), but gap-filling is required when complete time series are required for the derivation of daily, seasonal or annual integrals (Papale, 2012).

A range of gap-filling methods have been reported in the literature (mainly for CO_2). These include: mean diurnal variation (Falge *et al.*, 2001), artificial neural networks (Papale *et al.*, 2003), non-linear regressions (Desai *et al.*, 2005) and process-based models (Moffat *et al.*, 2007). Falge *et al.* (2001) and Moffat *et al.* (2007) showed most methods produced comparable results with error margins approaching the noise range of EC measurements. The choice of method ultimately depends on the length and distribution of data gaps, availability of prognostic (i.e. meteorological) data, and the balance between implementation costs and gap-filling performance (Papale, 2012). In the effort to standardise flux data handling, an online implementation of the high-performance method of Reichstein *et al.* (2005a) has been made available to the flux measurement community, and has been used across a variety of peatland environments (e.g. Hendricks *et al.*, 2007; Merbold *et al.* 2009; Lund *et al.*, 2010).

3.5 Flux partitioning

In terms of CO₂, EC system provides a direct measurement of NEE. Measurements of daytime NEE do not discriminate between GPP and ER (or between autotrophic and heterotrophic contributions to ER) (Reichstein *et al.*, 2005a; 2012). Improved processes knowledge is gained through statistical partitioning of NEE into its component fluxes (Reichstein *et al.*, 2005a; 2012; Lasslop *et al.*, 2010).

Numerous flux partitioning algorithms have been developed (e.g. Reichstein *et al.*, 2005a; Desai *et al.*, 2005; 2008; Lasslop *et al.*, 2010). The most widely used approach is based on extrapolating measurements of nocturnal NEE (representing ER only when photosynthesis is inactive) to daytime conditions as a function of temperature, with GPP estimated by difference (Desai *et al.*, 2005; Reichstein *et al.*, 2005a). Alternative

methods generate (single) estimates of daytime ER as the y-intercept of the light response of daytime NEE (Smith *et al.*, 2010a), although these have not been widely used in peatland studies.

Twenty-three flux partitioning algorithms were compared for forested ecosystems (Desai *et al.*, 2008). Most partitioning algorithms differed by less than 10% in estimates of annual GPP and ER. In the absence of independent validation, however, estimates of (daytime) ER and GPP derived from measurements of NEE should be treated as such, simultaneously representing best estimates and a known source of potential systematic bias (Richardson *et al.*, 2012).

3.6 Energy balance closure

Energy balance closure (EBC) is commonly used as a metric to assess EC system performance and the plausibility of EC datasets (Foken *et al.*, 2004; Burba & Anderson, 2012; Leuning *et al.*, 2012). EBC is an expression of the first (conservation) law of thermodynamics, which requires the sum of the turbulent energy fluxes (LE+H) balances the sum of all other energy terms (Wilson *et al.*, 2002). In simple terms (i.e. neglecting terms not or inadequately measured at EC sites) the surface energy balance is defined using:

$$R_{net} - G \approx H + LE \approx 0 \qquad 3.2$$

where: R_{net} is the net radiation (measured using a net radiometer); G is soil heat flux (measured using soil heat flux plates); H and LE are EC measurements of latent and sensible heat flux, respectively; all fluxes are in W m⁻².

As a plausibility test, EBC assumes that if the turbulent energy fluxes have been effectively quantified, then so too have trace gas fluxes (i.e. CO_2). In reality, full EBC is rarely (if ever) attained using EC, with 70% to 90% closure typically attained across a range of ecosystems (Wilson *et al.*, 2002; Foken *et al.*, 2006; Jacobs *et al.*, 2008; Leuning *et al.*, 2012). Various potential reasons for the energy imbalance exist (summarised in Table 3.3), some of which may influence trace gas measurements (Wilson *et al.*, 2002; Foken *et al.*, 2011; 2012). At the current time, consensus holds that while EBC remains an important test of plausibility (Burba & Anderson, 2012), it should not be used to correct trace gas flux measurements¹⁹ (Baldocchi, 2003; Foken *et al.*, 2011; 2012) as proposed by some authors (e.g. Twine *et al.*, 2000).

¹⁹ Reasons for not scaling trace gas fluxes to the energy balance include uncertainties in scalar similarity (Foken *et al.*, 2010; 2012) and requirements to place undue confidence on available energy sensors (i.e. net radiometers and soil heat flux plates) (Baldocchi, 2003).

Table 3.3: Potential reasons for the lack of energy balance closure measured using the eddy covariance technique

Potential cause	Description and relevance to CO ₂ flux measurements
Surface heterogeneity and advection	Surface heterogeneities within flux footprints or the wider landscape may generate low frequency turbulent motions or advective flux divergences that are not sampled by EC (Foken, 2008). Would also affect CO_2 flux measurements.
Sensor footprint mismatch	Energy balance (i.e. net radiometers and soil heat flux plates) have a footprint that does not match that of the time-varying footprint of EC measurements. Would not affect CO_2 flux measurements.
Instrument bias	Bias relating to available energy (e.g. net radiometers and/or heat flux plates) and/or EC measurement systems. Net radiation is typically the largest term in the EBC equation and measurement uncertainty could strongly influence closure, although there is little evidence for a systematic error in commonly used net radiometers (Leuning <i>et al.</i> , (2012) and references therein). Soil heat flux plates may be inaccurate under some conditions, particularly in organic soils (Laurila <i>et al.</i> , 2012). Bias in available energy sensors would not affect CO_2 flux.
	EC sensor bias (i.e. SATs, IRGAs) would lead to systematic error in EC energy flux measurements. Would affect CO_2 flux measurements via influences on flux processing routines, such as the propagation of error through the Webb, Pearman & Leuning (1980) density adjustment (Leuning <i>et al.</i> , 2012).
Neglected/poorly measured energy balance terms	Part of the energy imbalance reflects heat storage that is poorly (i.e. soil heat storage) or not measured at flux measurement sites (i.e. heat storage in the soil-plant-atmosphere layer, energy used in photosynthesis (Jacobs <i>et al.</i> , 2008)). Leuning <i>et al.</i> , (2012) showed EBC typically improved across sites when daily averages were used to evaluate closure, indicating storage effects are at least partly responsible for the energy imbalance. Would not affect CO_2 flux measurements.
High/low frequency spectral loss	Limitations in instrument geometry and the use of finite averaging periods can result in flux attenuation at high and low frequencies, respectively (Wilson <i>et al.</i> , 2002; Foken <i>et al.</i> , 2006). Would also affect CO_2 flux measurements.

3.7 Uncertainties affecting EC measurements

EC measurements and derived integrals (i.e. of NEE) are subject to random and systematic errors. Random measurement errors are largely related to instrument noise, footprint heterogeneity and the stochastic nature of turbulence (Richardson *et al.*, 2012), and become reduced (but do not vanish) with increasing sample size (Moncrieff *et al.*, 1996; Elbers *et al.*, 2011; Richardson *et al.*, 2012). Systematic errors (bias) may be selective (i.e. nocturnal flux underestimation, rejection of data during rainfall) or fully systematic (i.e. calibration errors, flux calculations, lack of EBC) (Richardson *et al.*, 2012). When used in a policy context (i.e. for land C accounting) or for influencing land management decisions, these potential sources of uncertainty must be assessed, and estimates of NEE presented within appropriate uncertainty bounds (Elbers *et al.*, 2011; Richardson *et al.*, 2012).

3.8 Chapter summary

This chapter has provided an overview of the micrometeorological EC technique. The EC measurement principle and instrumental requirements have been described. Details of the theoretical assumptions of the technique, and the post-processing corrections and adjustments required to meet these assumptions were provided. A summary of the quality control procedures typically used to reject data of poor quality was presented. A description of the methods used to fill unavoidable gaps in eddy covariance flux records and to partition measurements of NEE into its component fluxes (i.e. GPP and ER) was provided. The role of EBC as a means of assessing the plausibility of EC CO_2 flux measurements was discussed. A short overview of the random and systematic errors affecting EC measurements was provided.

Chapter Four: Materials and methods

This chapter provides details of the flux measurement sites and all instrumentation, ancillary datasets and data handling protocols used in this research. The chapter begins with an overview of the Wicken Fen National Nature Reserve (NNR) and the Wicken 100-year Vision. Descriptions of the site conditions and management practices at the semi-natural and regenerating ex-arable fen flux measurement sites are provided. A description and comparison of the EC and environmental instrumentation deployed at the two sites is given. All ancillary datasets used in the research are described.

The second part of the chapter details the EC data handling protocols employed. Details of all EC data post-processing and QC procedures are provided. The chapter presents a summary of NEE data coverage and availability. The methods used to fill gaps in the NEE flux time series and to partition NEE into its component fluxes are described. An evaluation of the data gap-filling method is provided for NEE. The plausibility of the EC flux measurements is evaluated by reconstructing the surface energy budget at both sites. Specific data analysis techniques used to address the research questions and objectives (Chapter 1) are described in respective results chapters.

4.1 Study site description

4.1.1 Wicken Fen and the Wicken Fen 100-year Vision

This research was conducted within the boundaries of the Wicken Fen National Nature Reserve (NNR) in the Cambridgeshire Fens (52°18'N, 0°16'E). Wicken Fen (WF) is located towards the southern fringe of the Fenland basin (Figure 1.1), approximately 20 km northeast of the City of Cambridge and directly south of the village of Wicken. The WF reserve is situated within a 27.6 km² catchment of low relief (maximum elevation

of 49 m amsl²⁰), dominated by intensive arable land use on peat soils (McCartney *et al.*, 2001). The WF main reserve (currently) exists as an island of semi-natural peatland (and biodiversity) surrounded by intensive agriculture (Moore, 1997; Friday & Colston, 1999; The National Trust, 2007).

The climate of the Fenland is one of the driest in the UK. Mean annual temperature²¹ is 10.4° C with an average yearly precipitation of 560 mm²². Precipitation is evenly distributed throughout a typical year. Potential evapotranspiration in 594 mm and typically exceeds rainfall between April and September (McCartney *et al.*, 2001; McCartney & de la Hera, 2004; Stroh *et al.*, 2012). South-westerly wind flow dominates throughout the year. Recent years have experienced strong variability in weather conditions relative to baseline climatic patterns (discussed in Chapters 5 and 8).

Wicken Fen (Figure 4.1, 4.2 and 4.3) is the largest of the four Fenland reserves (Figure 1.1) and contains *circa* 170 ha of semi-natural (i.e. relatively intact) calcareous peatland (Rowell & Harvey, 1988; Rowell, 1997; Hughes *et al.*, 2011). The site largely escaped widespread drainage efforts of the seventeenth century, due to the economic importance of its sedge harvest and later as a site of interest to Victorian naturalists (Rowell, 1997; Rowell & Harvey, 1988). WF occupies a central role in the history of British nature conservation and ecology, and is the site where Godwin developed seminal theories on hydroseral and deflected successions (e.g. Godwin & Bharucha, 1932; Godwin, 1936). In 1899, WF became the first UK site established specifically for purposes of nature

²⁰ meters above mean sea level

²¹ Mean annual temperature based on the thirty-year period 1979 to 2008 from the UK Met Office Station Cambridge NIAB (54°35'E, 00°26'N, 26 m OAD) approximately 20 km from Wicken Fen.

²² Mean annual precipitation based on the -year period 1979 to 2008 from the UK Met Office Rain Gauge Station in Stretham (52°33'N, 00°23'E, 4 m OAD) approximately 5.4 km from the study site.

conservation, making it one of the oldest UK nature reserves (Rowell, 1997; Stroh *et al.*, 2012).

The WF reserve is intensively managed to maintain a diversity of fenland habitats along the successional gradient from open water to woodland (Hughes *et al.*, 2011; Kelvin, 2011). WF has been continually expanded under the stewardship of the National Trust²³, from an original 0.6 ha in 1899 to a current area of *circa* 930 ha (Hughes *et al.*, 2011). The reserve supports an exceptional biodiversity, with over 8000 recorded species (Warrington *et al*, 2009). WF is designated a National Nature Reserve (NNR), a Site of Special Scientific Importance (SSSI), a Special Area of Conservation (SAC) under the European Habitats Directive, and a Ramsar Site of International Importance (The Convention on Wetlands of International Importance, 1971).

²³ The National Trust is the non-governmental organisation that owns and manages the Wicken Fen National Nature Reserve.

Map removed for copyright reasons

Figure 4.1: Map of the Wicken Fen National Nature Reserve showing the main fen compartments and watercourses. Note that the area called Priory Farm was brought into restoration management in 1994 and is now called Bakers Fen. Map source: McCartney *et al.* (2001).

Concerns over localised extinctions led to the launch of the Wicken Fen 100-year Vision in 1999 (The National Trust, 2007; Hughes *et al.*, 2011). The WF Vision (Figure 4.2) aims to acquire and restore *ca*. 5300 ha of arable land between the existing reserve and Cambridge by 2100, creating one of the largest restored wetlands in Europe (The National Trust, 2007; Hughes *et al.*, 2011). Over 44% (~2376 ha) of the proposed restoration will target degraded peat soils (Figure 4.2). A stated objective is to protect remaining peat soils from further depletion (The National Trust, 2007).

The Vision is an open-ended, landscape-scale project, aiming to create a dynamic wetland landscape, maintained by low-intensity management using natural

regeneration, self-reliant grazing herds and (where practicable) fluctuating water levels (Stroh *et al.*, 2012; Hughes *et al.*, 2011). At the time of writing, 390 ha were managed using this approach (Hughes *et al.*, 2011). An ongoing concern about the feasibility of the Vision relates to the availability of adequate water²⁴ in this agriculturally dominated landscape (Ness & Proctor Nichols, 2008; Hughes *et al.*, 2011).

Map removed for copyright reasons

Figure 4.2: Soil series map of the proposed Wicken Fen 100-year Vision Project Area. Map source: The National Trust (2007).

²⁴ At the time of writing in late summer 2012, the East Anglian region has recovered from a state of severe drought, followed by one of the wettest summers on record during 2012.

EC measurements were made at two sites within the WF reserve (Figure 4.1 and 4.2). One is an area of semi-natural fen (Wicken Sedge Fen - WSF). The other is part of the first area of agriculturally degraded fen to be brought under restoration management (an area of Adventurer's Fen known as Bakers Fen - BF). The sites are immediately adjacent, with a distance of *circa* 1 km between the flux tower installations. Both sites experience near-identical micrometeorological conditions. The study sites are described below.

Image removed for copyright reasons

Figure 4.3: Aerial image of the Wicken Fen Reserve Showing the locations of the flux towers. The location of the Wicken Sedge Fen flux tower is indicated by the orange star. The Bakers Fen flux tower is indicated by the red star. Image source: Google Earth (2011).

4.1.2 Wicken Sedge Fen

The Wicken Sedge Fen (WSF) site (incorporating part of Verrall's Fen in Figure 4.1) is a rich calcareous fen (pH ~7) that forms the nucleus of the WF NNR. WSF has not experienced significant drainage²⁵ and its surface lies approximately 2 m higher than surrounding agricultural land. The primary source of calcareous water is Wicken Lode²⁶, an embanked high level tributary of the River Cam (Figure 4.1). Water enters the site via an interconnected network of ditches. Historically, the site experienced regular flooding during the winter months. Since the 1940s, Lode levels have been regulated by a sluice at Upware²⁷ and the magnitude of winter flooding has declined (McCartney *et al.*, 2001).

Concern has been raised that WSF may be drying out during summer months relative to past conditions, although the mechanism remains unclear (McCartney and de la Hera, 2001; McCartney *et al.*, 2001; Kelvin, 2011). A new wind pump was installed at the site in 2010, with the aim of abstracting additional calcareous water from Monks Lode (Figure 4.1) during the winter months; however, the pump was not in use during the reported measurement period.

Soils at WSF are Adventurers series (sedge) fen peats overlying impervious Gault clay. Peat depth ranges from 1 to 4 m from east to west (Rowell & Harvey, 1988), and is *circa* 2 m at the location of the flux tower (Lester, personal communication). Soil organic matter (SOM) content (estimated by loss-on-ignition) is approximately 77% in

²⁵ Widely held assumptions that the Sedge Fen has never experienced drainage were challenged by Rowell (1994). Evidence of peat digging in some locations suggests areas of the ancient fen may have experienced some form of historical drainage.

²⁶ Wicken Lode is believed to be of Roman origin.

²⁷ At a pumping station at the confluence of Wicken Lode with the River Cam.

the upper 0.5 m of the peat profile (Morgan, 2005; Stroh *et al.*, 2012). Bulk density is approximately 0.2 g cm⁻³ to a depth of 0.5 m (Morgan, 2005).

Historically, WSF was managed by sedge harvesting, enabling the site to persist as open fen habitat (Rowell, 1994). A decline in traditional management over recent decades led to successional encroachment of carr woodland (Rowell & Harvey, 1988). More recently, scrub clearance and reinstatement of a traditional management regime has been successful in restoring open fen vegetation (Friday & Colston, 1999). Current vegetation management consists of rotational harvesting of small land parcels on a three/four year basis, creating a mosaic of stands of different ages and preventing further scrub encroachment.

Vegetation at WSF is dominated by saw sedge (*Cladium mariscus*) and common reed (*Phragmites australis*) corresponding with the *Symphytum officinale* sub-community of *Phragmites australis-Peucedanum palustre* tall-herb fen of the National Vegetation Classification (NVC classification S24c) (Rodwell, 1995). A small land parcel approximately 200 m east of the tower was cut during August (exact timing unknown) in both years. However, the area was small relative to the footprint of the flux tower and wind flow was typically from the south-west during these periods, and unlikely to have significantly influenced flux measurements. It is noted that full C accounting would require estimates of the amount of C removed by cutting; however, this export term was not measured and is subsequently not included here.

The WSF site was instrumented by researchers from the Centre for Ecology and Hydrology (CEH, Wallingford) in 2009. The available fetch is limited to approximately

150 m to the north of the EC tower by an area of woodland, but extends to approximately 400 m for all other wind sectors. Data coverage was intermittent during the winter months due to inadequate electrical power. Measurements are reported from 20^{th} March to 31^{st} December for 2009 and 2010.

4.1.3 Bakers Fen

The Bakers Fen (BF) site (Priory Farm in Figure 4.1) is a 55 ha former arable fen located immediately adjacent²⁸ to WSF. BF forms part of a wider area known as Adventurers Fen. The site was initially drained in the mid-nineteenth century (1840) and used for intensive cereal and row crop production in decades prior to restoration (Friday & Chatfield, 1997; Friday & Colston, 1999). BF was taken out of arable production in 1993 and has developed into semi-natural grassland (see Figure 4.4). Initial restoration measures in 1994²⁹ involved ditch re-profiling, excavation of a number of scrapes³⁰ and replanting with native grassland species (Friday & Chatfield, 1997). Links to the agricultural drainage network were severed at this time, except at one location where water levels can be controlled by sluice. Rewetting commenced in 1998 and is achieved via the existing agricultural drain and ditch network (Lester, personal communication). The hydrology of the wider Adventurers Fen restoration area remains poorly understood (Lester, personal communication).

²⁸ The distance between the two flux towers is approximately 1 km

²⁹ The Bakers Fen site forms part of the Wicken Fen Vision land, but initial attempts to restore the site in 1994 predate the launch of the Wicken Vision in 1999.

³⁰ Small areas excavated to enhance the habitat diversity of the site.

Current management consists of abstractions of calcareous water from Monks Lode (Figure 4.1) and low density conservation grazing by highland cattle (23 LSU³¹) and wetland-adapted Konig Ponies (46 LSU). Summer water rights are fully allocated to the surrounding agricultural land use; abstractions are only possible between 1st November and 31st March (Lester, personal communication). A total of 95104.88 m³ was abstracted onto Adventurers Fen³² between November 2009 and March 2010 (Lester, personal communication). Growing season water levels reflect the balance between water stored over winter and the meteorological water budget. It was not possible to determine when animals were present within the EC footprint, but acknowledged that animal respiration was captured by flux measurements. The animals are present on the site throughout the year and no C is currently³³ exported in animal products. It was assumed that animals spend an equal amount of time in all areas of the site. All biomass consumed on site is subsequently deposited (as faeces and urea) and respired *in situ*.

The surface of BF (Figure 4.3) is a mosaic of semi-natural grassland communities intersected by drainage ditches at variable spacing (*circa* 100 to 200 m). The surface was approximately estimated to consist of ~60% rough grassland in relatively dry areas, ~30% perennially saturated areas (including scrapes), and ~5% ditches. Areas of bare peat are also present to limited extent. Dominant species³⁴ in relatively dry areas are: couch grass (*Elytrigia repens*), cocksfoot (*Dactylis glomerata*), false oat-grass (*Arrhenatherum elatius*), rough bluegrass (*Poa trivialis*) and creeping bent (*Agrostis*)

³¹ LSU - Livestock units

³² This represents the wider area under restoration management, which includes the Bakers Fen study site.

³³ The National Trust is considering the economic potential of marketing free-range cow and horse meat in the future

³⁴ Species data provided by Peter Stroh of Anglia Ruskin University

stolonifera). Hawthorn (*Crataegus monogyna*) is present as an occasional species. Ephemerally wet areas are dominated by soft rush (*Juncus effusus*), hairy sedge (*Carex hirta*) and *A. stolonifera*. *Phragmites australis* is dominant in ditch communities.

Extensive peat wastage has occurred across BF and the surface elevation lies approximately 1.5-2 m below WSF (Ness & Proctor-Nichols, 2008). A slight elevation gradient exists from east to west (not measured). Soils are highly degraded Adventurers series peats overlying Gault clay. Residual peat depth was surveyed³⁵ in May 2011. Mean peat depth is *circa* 0.55 m (SD=0.63 m; range=0.38-0.81 m; n=196) with areas of deeper peat to the south and west of the site. Considerable spatial variation in peat moisture conditions was observed during the survey, wetter areas corresponding with deeper peat. SOM in the upper 0.3 m of the peat profile is approximately 34% (Morgan, 2005; Stroh *et al.*, 2012). pH is approximately 7.1 (Hardy, personal communication). Peat bulk density is around 1.1 g cm³ (Ness & Proctor-Nichols, 2008).

The BF instrumentation was installed on a slightly elevated³⁶ (on the order of a few cm) location close to a ditch edge during October 2009. The minimum available fetch is 260 m to the north and west of the tower, at least 400 m in all other directions, over 600 m along the prevailing (south-westerly) wind direction. In this thesis, flux measurements are reported for the complete annual cycle of 2010, as the flux tower did not become fully operational until late December 2009.

³⁵ GPS locations were collected at this time using ArcPad (ESRI, California, US) running on an HTC Smartphone; however, a technical problem occurred during data transfer resulting in the loss of the spatial data. It was not therefore possible to produce a peat depth map.

³⁶ The location of the tower was constrained by the management objectives of the site. Conditions of the installation were that the tower was installed close to a ditch boundary away from open areas. The slightly elevated location was selected to minimise the chance of the electronics box becoming flooded.

4.2 Instrumentation

4.2.1 Wicken Sedge Fen

The EC system at the WSF site (right in Figure 4.4; Table 4.1) comprises an omnidirectional Gill Instruments R3 SAT (Gill Instruments, Lymington, UK) and a LI-COR Biosciences Li7500 open-path H_2O/CO_2 IRGA (LI-COR Inc., Lincoln, Nebraska, USA). Barometric pressure was measured near the base of the tower in the Li7500 control box. The Li7500 was positioned below and to the southwest of the R3. Separation distance between R3 and IRGA was 0.3 m. The Li7500 was tilted at an angle of approximately 15° to prevent water accumulation in the optical path. The EC instrumentation was installed on a steel tripod at 4 m above the fen surface (double the mean vegetation height).



Figure 4.4: Wicken Sedge Fen eddy covariance system (left) and automated weather station (AWS; right). The left image shows the omni-directional R3 sonic anemometer-thermometer and Li7500 infrared gas analyser, HMP45 probe and CNR1 net radiometer. The right image shows the various temperature and relative humidity, wind speed and direction and radiation sensors installed on the AWS. White weatherproof boxes house dataloggers and instrument control boxes. Images acquired by the author in December 2009.

A range of environmental measurements were made at WSF (Table 4.1). The net radiation (R_{net} ; W m⁻²) and its components were measured using a CNR1 net radiometer (Kipp & Zonen, The Netherlands) installed at 3.5 m on the EC tripod. The CNR1 was orientated southwards to prevent shading. Soil heat flux was measured using two HFP01SC self-calibrating heat flux plates (Hukesflux, Delft, The Netherlands) installed at 0.08 m below the fen surface. Air temperature (T_{air} ; °C) and relative humidity (RH; %) were measured using a HMP45 probe (Vaisala, Helsinki, Finland) encased within an aspirated radiation shield. All aforementioned instruments were scanned at 20 Hz and logged using a CR3000. Power to the system was provided by an array of solar panels and a bank of 12 v leisure batteries. An automated weather station (AWS) was installed at the site (right in Figure 4.3 providing additional measurements of net radiation, 2 m air temperature and relative humidity (using a HMP45 probe).

Water level position relative to the fen surface was monitored at two automated dipwells approximately 100 m south of the flux tower. Hourly data from these dipwells were provided by the UK Environment Agency. Data from the two dipwells were in good agreement and averaged to provide a single time series. Data were linearly interpolated to thirty minute periods to match EC and meteorological measurements. No precipitation, peat temperature or volumetric peat moisture content (θ_{peat}) measurements were made at WSF (Table 4.1).

Measured variable (notation)	Unit	Wicken Sedge Fen	Bakers Fen
3D wind speed (u, v, w) and sonic temperature (10/20 Hz)	m s ⁻¹ /°C	R3 sonic anemometer thermometer (Gill Instruments, Lymington, UK)	CSAT3 sonic anemometer thermometer (Campbell Scientific, Shepshed, UK)
H ₂ O/CO ₂ concentration (10/20 Hz)	$mg \; CO_2 \; m^{\text{-}3}\!/g \; H_2O \; m^{\text{-}3}$	Li7500 H ₂ O/CO ₂ infrared gas analyser (LI-COR Biosciences, Lincoln, US)	Li7500 H ₂ O/CO ₂ infrared gas analyser (LI-COR Biosciences, Lincoln, US)
Barometric pressure	KPa		
Air temperature (T_{air}) and relative humidity (RH)	°C/%	HMP45 air temperature and relative humidity probe (Vaisala, Helsinki, Finland). Measurements duplicated by HMP45 on AWS	HMP45 air temperature and relative humidity probe (Vaisala, Helsinki, Finland).
Net radiation (R_{net}) and incoming and outgoing long- and shortwave radiation	W m ⁻²	CNR1 net radiometer (Kipp & Zonen, Delft, The Netherlands)	CNR1 net radiometer (Kipp & Zonen, Delft, The Netherlands)
Soil heat flux (G)	W m ⁻²	2 x HFP01SC self-calibrating heat flux plates installed at 0.08 m (Hukesflux, Delft, The Netherlands)	3 x HFP01SC self-calibrating heat flux plates installed at 0.08 m (Hukesflux, Delft, The Netherlands)
Photosynthetically active radiation (PAR)	μ mol m ⁻² s ⁻¹	Not measured. Estimated from global radiation channel of CNR1 and BF Quantum Sensor	Quantum sensor (Skye Instruments, Llandrindod Wells, UK)
Peat temperature (T _{peat})	°C	Not measured	4 x TCAV averaging thermocouples (Campbell Scientific, Shepshed, UK)
Volumetric peat moisture content (θ_{peat})	m ⁻³ m ⁻³	Not measured	3 x CS616 water content reflectometers (Campbell Scientific, Shepshed, UK)
Precipitation (P)	mm	Not measured	ARG100 Tipping Bucket Rain Gauge (Campbell Scientific, Shepshed, UK)
Water level relative to fen surface	cm	Measured in two automated dipwells operated by the UK Environment Agency	Three divers plus one barodiver (ECO Environmental, Perth, Australia)

Table 4.1: Summary and comparison of environmental sensors used at the Wicken Sedge Fen and Bakers Fen flux measurement sites.

4.2.2 Bakers Fen

The BF EC system (Figures 3.1 and 4.4; Table 4.1) consists of a Campbell Scientific CSAT3 three-dimensional SAT (Campbell Scientific Ltd., Shepshed, UK) and Li7500 IRGA (LI-COR Inc., Lincoln, Nebraska, USA). The EC system was installed at 2.35 m above the fen surface on a steel tripod. The measurement height was selected to maximise the available fetch for all wind sectors (assuming a 100:1 fetch to height ratio), and to be over twice the maximum summer vegetation height (Foken, 2008). The Li7500 was positioned below and to the southwest of the CSAT3 and tilted to encourage runoff. Spatial separation between the Li7500 and CSAT3 was 0.13 m. High frequency EC data were logged using a CR3000 datalogger (Campbell Scientific Ltd., Shepshed, UK).



Figure 4.5: Bakers Fen eddy covariance station. The image shows the eddy covariance system (centre back) comprising a Li7500 IRGA and Campbell Scientific CSAT3, the green electronics box and solar panels, and the CNR1 net radiometer at front). White weatherproof boxes house the dataloggers and instrument control boxes. Image acquired by the author on 28th June 2010.

A range of environmental measurements were made at BF using identical sensors to those deployed at WSF. (Table 4.1). R_{net} and its components were measured using a CNR1 net radiometer (Kipp & Zonen, Delft, The Netherlands). The CNR1 was mounted at 2.35 m on a separate mast 7.5 m east of the EC system (Figure 4.4) and orientated southwards. Soil heat flux (G; W m⁻²) was measured using three HFP01-SC heat flux plates (Hukesflux, Delft, The Netherlands) installed at 0.08 m below the fen surface. T_{air} and RH were measured at 2 m using a HMP45 sensor (Vaisala, Helsinki, Finland) encased in an aspirated radiation shield (Campbell Scientific Ltd., Shepshed, UK).

A number of environmental measurements not obtained at WSF were made at BF (Table 4.1). Photosynthetically active radiation (PAR; μ mol m⁻² s⁻¹) was measured using an SKP215 Quantum Sensor (Skye Instruments, Llandrindod Wells, UK) installed on the EC tripod and orientated to prevent shading. Peat temperature (T_{peat}; °C) was measured at depths of 0.05, 0.15 and 0.3 m using TCAV averaging thermocouples (Campbell Scientific, Shepshed, UK). A further TCAV was installed to measure peat temperature in the peat layer above the HFP01SC. Precipitation (P; mm) was measured using an ARG100 tipping-bucket rain gauge (Campbell Scientific, Shepshed, UK).

 θ_{peat} was measured using three CS616 time domain reflectometers (Campbell Scientific Ltd., Shepshed, UK). One CS616 was inserted horizontally at 0.05 m; the remaining two inserted vertically in the upper 0.3 m of the peat profile. Similar to Lafleur *et al.*, (2005), it was not possible to determine a CS616 laboratory calibration for use in peat soils (despite repeated attempts). CS616 data were therefore considered a relative measure of θ_{peat} (Lafleur *et al.*, 2005). An unresolved problem was encountered with all

CS616 sensors when clearly non-physical values were recorded (rapid fluctuations approximating a square wave). Data for these periods were excluded from analyses.

Two dataloggers were used at BF. HMP45, TCAV CS616 and HFP01 sensors were scanned at 20Hz and logged on the CR3000. All other sensors were scanned at 5 s and stored as thirty minute averages using a CR1000 Measurement and Control System (Campbell Scientific Ltd., Shepshed, UK). Datalogger clocks were synchronised during each site visit. Time drift was never more than a few seconds. All loggers (including the WSF CR3000) were set to Greenwich Mean Time (GMT) for the duration of the measurement period.

Power to the BF system was provided by two 250 W solar panels and two 6 v batteries (Solar-wind Ltd, Ipswich, UK). Electronics were housed in a green locker located north of the EC tower (Figure 4.5). The instrumentation was enclosed within a 1 m post and barbed wire fence to prevent damage by (or to) the grazing herd. A limitation of the installation was that the solar panels and electronics box, EC tower and a fence post were within the field-of view of the CNR1 (see Figure 4.5). Grass within the compound was clipped intermittently so the vegetation (below the CNR1 and above the HFP01-SC) better reflected conditions of the grazed site.

The position of water levels relative to the fen surface was monitored using three selflogging divers and one barodiver (Schlumberger Water Services, Canada). Divers were installed within perforated plastic tubes anchored into the Gault clay. One of the divers and the barodiver were installed at the location of the flux tower. The remaining two were installed in open locations south of the tower. Divers were logged at two hourly intervals. Similar to WSF, diver measurements were linearly interpolated to provide thirty minute averages.

4.2.3 Li7500 calibrations

It was not possible to calibrate the Li7500 gas analysers at a desired frequency during this research. This was due to a lack of calibration facilities at the home institution. A number of calibration attempts were considered unreliable and were not accepted. To ensure the accuracy of measurements, a linear correction was applied to Li7500 H₂O and CO₂ concentration measurements between accepted calibrations. Full details of the Li7500 calibrations are provided as Appendix A. It is accepted that such a correction is only truly valid if sensor drift is linear (e.g. Richardson *et al.*, 2012). However, drift in CO₂ sensor gain was never greater than 3% at either site (Appendix A). In the absence of calibration facilities, a linear correction was considered the most appropriate means of ensuring the reliability of the flux estimates.

4.3 Ancillary datasets

4.3.1 Climate data

No long-term meteorological record is available for Wicken Fen. To enable comparisons against longer-term climatic patterns, additional meteorological data were obtained from two UK Met Office Stations. Monthly data on (2 m) air temperature and the number of days with air frost were obtained from the Met Office NIAB station in Cambridge (54°35'E, 00°26'N, 26 m amsl) situated approximately 20 km from WF. Monthly precipitation data were obtained from a Met Office rain gauge in Stretham (52°33'N, 00°23'E, 4 m amsl) located approximately 5 km from WF. Monthly average T_{air} data from Cambridge NAIB differed slightly to values measured at WF, but was considered adequate for comparing T_{air} conditions during the measurement period with longer-term averages. Monthly P data from Stretham showed good general agreement with monthly sums measured at BF (see Table 5.1). Monthly meteorological data for the thirty year period 1979 to 2008 were used to define baseline climatic conditions.

4.3.2 Vegetation datasets

To characterise seasonal changes in the phenology of the BF vegetation, one-sided LAI (m² m⁻²) was measured at approximately fourteen day intervals between 13th May and 13th October 2010. No measurements were available at WSF. LAI measurements were made with a Sunscan Canopy Analysis System (SCAS) and BF3 Sunshine Sensor (Delta-T Devices Ltd., Burwell, UK) using default instrument settings provided for rye grass (*Lolium perenne*).

LAI measurements were made at four locations within the tower footprint. Measurements were restricted to the dominant grassland community present at the site due to practical difficulties in measuring *J. effusus* and ditch communities. Depending on time availability, between 20 and 40 individual measurements were made at each location within a *circa* 15 m radius (due to the length of the SCAS cable). At each measurement point, the SCAS wand was inserted below the grass canopy as close and as parallel to the surface as possible. Data were logged on a PSION Workabout hand held computer (PSION Plc. London, UK). LAI data obtained on each day were bulked to provide a single spatial average to match the scale of EC measurements. Seasonal change in BF LAI was modelled using a Gaussian function, as:

$$LAI(JD) = LAI_{max} * exp\left(-\left(\frac{JD - JD_{max}}{c}\right)^{2}\right)$$
4.1

where: LAI_{max} is the maximum seasonal LAI, JD denotes Julian Days (days 1 to 365 in any non-leap year); JD_{max} is the JD when LAI_{max} is attained; parameter *c* determines the width of the fitted curve. Fits were computed using the Curve Fitting Toolbox (Levenberg–Marquardt algorithm) of Matlab version 7.9.0.529, R2009b (The MathWorks Inc. Natick, Massachusetts, US).

Measurements of vegetation height are required to calculate the zero plane displacement height (*d*) for use in EC data post-processing and footprint analysis (Scheupp *et al.*, 1990; Foken, 2008). At BF, measurements of vegetation height were made at each LAI sampling location. Similar to the estimate of BF LAI, all vegetation height measurements were averaged to provide a single time series. Temporal change in growing season vegetation height (for use in flux processing and footprint analysis) was estimated by linearly interpolating between available measurements. Vegetation height was set to 0.2 m for the non-growing season. No vegetation height measurements were made at WSF. However, stems remain standing following senescence (Figure 4.4) and mean vegetation height remains approximately constant at 2 m throughout the year.

As a means of monitoring the phenology of WSF (and as an additional means of monitoring at BF), remotely sensed enhanced vegetation index (EVI) data were obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) platform. EVI is a dimensionless vegetation index (ranging from 0 to 1) increasingly used as a proxy for the phenology development and activity of terrestrial vegetation (Rocha & Shaver, 2009). As the purpose of the EVI data is to provide ancillary information on the

seasonal change in phenology, a full description of the MODIS platform and EVI algorithm lies beyond the scope of this thesis.

Three representative 250 m² resolution EVI pixels were downloaded from the MODIS website³⁷. Each pixel represents a sixteen-day composite obtained by the MODIS instrument on the Terra platform. Any clearly erroneous EVI values (i.e. large spikes) were discarded on the basis of visual inspection. To reduce potential contamination effects resulting from pixel misalignment, the three sixteen-day composites were averaged to provide a single value for each sixteen-day composite period. Similar to BF LAI, temporal change in MODIS EVI was modelled by fitting EVI data to a Gaussian function (of the same form as equation 4.1).

4.4 Data handling

4.4.1 Eddy covariance data processing

High frequency (10 and 20 Hz) EC data were post-processed using the EdiRe Data Software Package (version 1.5.0.28) of the University of Edinburgh³⁸. All fluxes were computed as block averages over thirty minute averaging periods using standard flux processing techniques (Mauder *et al.*, 2008). With the exception of an angle-of-attack dependent calibration that was applied to correct R3 data for transducer self-shading (Gash & Dolman, 2003), identical flux processing routines were used for both measurement sites. At WSF, vegetation height was set constant at 2 m. At BF, a file containing linearly interpolated estimates of seasonal change in vegetation height was

³⁷ available at: http://daac.ornl.gov/cgi-bin/MODIS/GLBVIZ_1_Glb/modis_subset_order_global_col5.pl

³⁸ available at: http://www.geos.ed.ac.uk/abs/research/micromet/EdiRe/

imported into EdiRe and used to calculate *d*. *d* was approximated as 0.64 times the mean vegetation height (Foken, 2008).

The EdiRe flux processing routine was developed from a processing list provided by the author of EdiRe (Clement, personal communication). Raw (20 Hz) data were tested for physical and electrical consistency (Table 4.2) and despiked (Vickers & Mahrt, 1996). SAT data were rotated into the planar fit coordinate frame (Wilczak *et al.*, 2001). The angle-of-attack dependent correction was applied to the WSF R3 data prior to the rotation procedure (Gash & Dolman, 2003). Rotation coefficients were calculated³⁹ separately for 2009 and 2010 at WSF. At BF, coefficients were calculated between periods when the position of the CSAT3 had been altered during tower maintenance.

Variable	Unit	Minimum	Maximum
Horizontal wind speed (u, v)	m s ⁻¹	-20	20
Vertical wind speed (w)	m s ⁻¹	-10	10
CO ₂ concentration	ppm	300	600
H ₂ O vapour concentration	g m ⁻³	0.1	18
Temperature	°C	-20	50

Table 4.2: Physical consistency limits used in eddy covariance data post-processing.

High frequency T_{air} fluctuations were calculated from the speed-of-sound measurements of the SATs (Schotanus *et al.*, 1983). The latent heat of evaporation and sensible heat flux coefficient were computed for each thirty minute period (Mauder et al., 2008). Uncorrected turbulent fluxes of H, LE and CO₂ were calculated following a cross-

³⁹ Planar fit coefficients were calculated using the Spreadsheet available at the EdiRe homepage: http://www.geos.ed.ac.uk/abs/research/micromet/EdiRe/Tutorials/EdiRe_Tutorial_12/

correlation procedure to remove sensor lags and maximise covariances (Mauder *et al.*, 2008; Foken, 2008). Turbulent fluxes of H, LE and CO_2 were corrected for limitations in the dynamic frequency response of the EC system (Moore, 1986). Final turbulent fluxes of LE and CO_2 were computed using the Webb, Pearman & Leuning (1980) adjustment for atmospheric density fluctuations.

Storage of CO₂ below the measurement height (F_s) was estimated from successive Li7500 CO₂ concentration measurements (Papale *et al.*, 2006). F_s was calculated using the storage calculation function of EdiRe. At both sites, and similar to other studies (e.g. Lafleur *et al.*, 2001; Merbold *et al.*, 2009), F_s was typically an order of magnitude smaller than the turbulent CO₂ exchange, becoming greatest around transitional periods at dusk and dawn. Final storage corrected NEE was computed as the sum of the turbulent CO₂ exchange and F_s (Aubinet *et al.*, 2000; Papale *et al.*, 2006).

4.5 Quality control

4.5.1 Outlier removal and technical data quality

QC procedures involved removal of statistical outliers and tests that the theoretical assumptions of the EC technique were not violated significantly. Data were removed during periods of unfavourable meteorological conditions. All flux data (H, LE and NEE) were filtered using the median absolute deviation (MAD) method described by Papale *et al.* (2006). Day- and night-time periods were treated separately using a moving window of 13 days and the recommended *z*-value of 5.5 (Papale *et al.*, 2006).

To ensure technical quality, fluxes were discarded when stationarity and integral turbulence test results were >100% above ideal values (Foken & Wichura, 1996; Foken

et al., 2004; Elbers *et al.*, 2011). At BF, data were discarded when the Li7500 AGC parameter⁴⁰ was over 20% of its baseline value (Ruppert *et al.*, 2006). AGC was not logged at WSF and data were rejected when >1% raw Li7500 H₂O data were filtered prior to flux computations. These latter criteria proved effective in excluding data when Li7500 and SAT measurements became unreliable during precipitation events.

4.5.2 Friction velocity threshold

Periods of low turbulent mixing were identified using a u^* threshold following methods similar to Lohila *et al.*, (2011). Nocturnal (R_g<20 W m⁻²) NEE (representing ER only) data were binned into u^* classes of 0.05 m s⁻¹ and averaged (Figure 4.6). The u_* threshold was identified as the upper bound of the u^* class where the mean was less than 95% of the mean of higher u^* classes (Papale *et al.*, 2006). At both sites, a u^* threshold of 0.1 m s⁻¹ was identified on this basis (Figure 4.6). All thirty minute flux data for periods when u^* was below this value were excluded from further analysis (with the exception of the assessment of uncertainty in time-integrated NEE discussed below). Turbulent energy fluxes (LE and H) were also discarded below this u^* threshold.

⁴⁰ A measure of the cleanliness of the Li7500 optical path. The AGC parameter typically increases above its baseline value during rainfall and other precipitation events.



Figure 4.6: Mean nocturnal net ecosystem exchange plotted against friction velocity (u^*) for the Wicken Sedge Fen (left) and Bakers Fen (right) flux measurement sites. NEE data were grouped into u^* bins of 0.05 m s⁻¹ and averaged. Error bars show standard errors for each u^* bin. Vertical dotted lines indicate the 0.1 m s⁻¹ u^* threshold used to reject data. Note different ordinate scaling (figures after Lohila *et al.*, 2011).

4.5.3 Flux footprint calculations

To assess the spatial representatives of the flux measurements, a source area analysis was conducted using the analytical footprint model of Scheupp *et al.* (1990). The relative contribution from each point in upwind of the measurement location (f) was calculated for each thirty minute period, using:

$$f(x_L) = \frac{U(z-d)}{u_* k x^2} e^{-(U(z-d0)/k u_* x)}$$
4.2

(Scheupp *et al.*, 1990; Burba & Anderson, 2011) where: *u* is the mean horizontal wind speed (m s⁻¹); z_m is the measurement height (m); *d* is the zero plane displacement (m); k is the von Karman constant (set to 0.4); and x_L is the upwind distance from the tower (m). Vegetation height was set to 2 m at WSF. At BF, calculations were performed using linearly interpolated field measurements of vegetation height. Footprints were calculated at a horizontal resolution of 1 m. Fluxes were considered representative and retained when integration of equation 4.2 along x_L indicated 75% of the measured flux

originated from the target ecosystem. This threshold is higher than the 70% criteria used by other wetland EC studies (e.g. Lohila *et al.*, 2011). The distance to the peak location (X_{max}) contributing to the measured fluxes was estimated using:

$$X_{max} = \frac{U(z_m - d)}{2ku^*}$$

$$4.3$$

(Scheupp *et al.*, 1990; Marcolla & Cescatti, 2005) where all variables were defined above. Hypothetical examples of the relative and cumulative contributions to the measured fluxes at WSF and BF are provided in Figure 4.7.



Figure 4.7: Examples of the relative and cumulative contributions to the measured flux. Footprints were estimated using the Scheupp *et al.* (1990) flux footprint model for Wicken Sedge Fen (black lines) and Bakers Fen (green lines). Footprint calculations were conducted using a mean wind speed of 5 m s⁻¹ and a friction velocity 0.5 m s⁻¹. The peak contribution contributing to the measured flux is indicated for Bakers Fen in the top panel.

Of the measurements retained for analysis after QC procedures, footprint calculations indicated the average distance to X_{max} (± standard deviation - SD) was 25 (±6.7) m and 28 (±7.4) m for WSF and BF, correspondingly. As a final check on data quality, all (LE, H and NEE) data were plotted for visual inspection at fortnightly intervals. Any clearly erroneous data (i.e. net CO₂ assimilation at night) were discarded (and assigned to the poor technical quality category described below).

4.6 Data coverage and availability

NEE data were lost at WSF due to system malfunctions and QC protocols (Figure 4.8). On a number of occasions, an undiagnosed malfunction led to unreadable raw 20 Hz data files. Thirty minute meteorological data were unaffected on these occasions as they are logged as separate CR3000 files. Missing data accounted for 10 and 15% loss of the potentially available measurements at WSF in 2009 and 2010, respectively. A relatively large fraction of the potentially available measurements were removed by the outlier detection routine (15 and 13% in 2009 and 2010, respectively). This likely reflects the use of an open-path EC system in this wetland environment. Data of poor technical quality (i.e. stationarity and integral turbulence tests, and raw data filtering) and application of the u^* filter led to removal of 12 and 5% data in both years correspondingly. Only 3% and 4% of data were removed on the basis of footprint analysis, correspondingly, as large footprints were generally associated with low turbulent mixing and rejected on this basis.

High quality NEE data coverage at WSF was within the range typically attained at other flux measurement sites (Falge *et al.*, 2001). A summary of monthly and total data

coverage is provided in Table 4.3. The length and distribution of long data gaps (> 1 day) is summarised in Table 4.4. Total data retained for analysis at WSF was 55 and 54% of all potentially available thirty minute periods of the 2009 and 2010 measurement periods, respectively (Figure 4.8; Table 4.3). NEE data coverage was higher during daytime periods than at night (Table 4.3), with 65 and 67%, and 45 and 42% of all potentially available day- and night-time measurement periods retained for 2009 and 2010, respectively. The pattern was similar at the monthly timescale (Table 4.3).



Figure 4.8: Charts showing data availability and data loss due to different causes at the Wicken Sedge Fen and Bakers Fen flux measurement sites. Values are shown as percentages of all potentially available thirty minute flux averaging intervals. The top charts show data coverage and loss for Wicken Sedge Fen for the period 20th March to 31st December during 2009 (left) and 2010 (right). The lower right chart show data coverage and loss at Bakers Fen during 2010.

At BF, missing data accounted for 9% of all data loss during 2010 (Figure 4.8). Missing data during January was caused by a solar charge convertor failure, although power to meteorological sensors was maintained on battery power during this time. The long data gap in June was due to bird foul on the Li7500. In December, failure of an internal CR3000 battery resulted in flux data loss from 16^{th} December onwards. Similar to WSF, a large number of measurements (17% of all potentially available data) were removed on the basis of the outlier detection routine. 17% of the annual dataset was identified as being of poor technical quality (i.e. on the basis of ITT, stationarity and AGC tests). Application of u^* and footprint criteria resulted in removal of a further 7 and 2% of potentially available measurements, correspondingly.

Total data coverage at BF during 2010 was 48% of all potentially available measurements (Table 4.3). Data coverage was low during the cold months, when large amounts of data were lost due to unfavourable measurement conditions (i.e. snow and frost). Similar to WSF and other sites, data coverage was higher during daylight periods than at night (except during December), with day- and night-time data coverage of 62 and 36%, respectively (Table 4.3). The distribution of long data gaps at BF are summarised in Table 4.4.
Table 4.3: Summary of monthly and total data coverage at the Wicken Sedge Fen and Bakers Fen flux measurement sites. Percentage of the potentially available thirty minute periods are shown in parenthesis. Data for March at Wicken Sedge Fen (marked with an *) represent the data available for the period 20^{th} to 31^{st} March in 2009 and 2010. Totals for the period represent 20^{th} March to 31^{st} December at Wicken Sedge Fen and for 2010 at Bakers Fen.

	Wicken Sedge Fen						Bakers Fen		
-		2009			2010			2010	
-	Total	Day	Night	Total	Day	Night	Total	Day	Night
January							306 (21) 111 (27)	195 (18)
February							485 (36) 222 (48)	263 (30)
March	144 (25)*	67 (24)*	77 (26)*	196 (31)*	92 (32)*	104 (31)*	422 (28) 264 (40)	158 (19)
April	710 (49)	458 (59)	252 (38)	629 (44)	432 (56)	197 (30)	782 (54	516 (67)	266 (40)
May	1088 (73)	718 (80)	370 (63)	918 (62)	697 (78)	221 (37)	851 (57) 672 (75)	179 (30)
June	896 (62)	673 (73)	223 (43)	809 (56)	666 (73)	143 (27)	756 (53	576 (63)	180 (34)
July	950 (64)	651 (71)	299 (52)	1004 (67)	731 (78)	273 (48)	1079 (73	i) 781 (85)	298 (52)
August	856 (58)	563 (67)	293 (45)	913 (61)	578 (70)	335 (50)	919 (62	582 (71)	337 (50)
September	690 (48)	414 (60)	276 (37)	834 (58)	474 (69)	360 (48)	816 (57	482 (71)	334 (44)
October	731 (49)	327 (57)	404 (44)	987 (66)	402 (70)	585 (64)	969 (65) 414 (72)	555 (61)
November	861 (60)	303 (67)	558 (56)	776 (54)	283 (63)	493 (50)	808 (56) 289 (65)	519 (52)
December	673 (45)	224 (58)	449 (41)	377 (25)	114 (28)	263 (24)	204 (14) 54 (13)	150 (14)
Total for period	7599 (55)	4398 (65)	3201 (45)	7435 (54)	4467 (67)	2968 (42)	8397 (48	4963 (62)	3434 (36)

Wi	cken Sedge Fen		Bakers Fen				
Start date (time)	End date (time)	Length (days)	Start date (time)	End date (time)	Length (days)		
25 th March 2009 (11:00)	27 March 2009 (15:00)	2.2	10 th January 2010 (07:30)	15 th January 2010 (12:00)	4.8		
28 th March 2009 (12:30)	9 th April 2009 (12:00)	12	19 th January 2010 (12:30)	25 th January 2010 (14:00)	6.1		
27 th August 2009 (12:00)	8 th September 2009 (18:00)	12.3	27 th February 2010 (16:00)	29 th February 2010 (18.30)	2		
12 th November 2009 (12:30)	14 th November 2009 (07:30)	1.8	16 th March 2010 (06:00)	20 th March 2010 (10.30)	4.4		
22 nd March 2010 (14:30)	24 th March 2010 (14:30)	2	20 th May 2010 (16:00)	22 nd May 2010 (07:30)	1.7		
26 th March 2010 (11:30)	28 th March 2010 (12:00)	2	24 th June 2010 (07:30)	31 st June 2010 (12:00)	6.2		
30 th March 2010 (12:30)	7 th April 2010 (10:30)	7.9	14 th November 2010 (22:00)	16 th October 2010 (13:00)	1.6		
27 th April 2010 (12:00)	29 th April 2010 (12:00)	2	1 st December 2010 (06:30)	7 th December 2010 (14:00)	6.3		
20 th July 2010 (18:30)	22 July 2010 (12:00)	1.8	16 th December 2010 (19:00)	31 st December 2010 (00:00)	15.2		
4 th November 2010 (12:00)	7 th November 2010 (06:30)	2.8					
16 th December 2010 (10:15)	20 th December 2010 (13:30)	4.1					
20 th December 2010 (22:00)	31 st December 2010	11					

Table 4.4: Distribution of long data gaps (> 1 day) at the Wicken Sedge Fen and Bakers Fen flux measurement sites.

4.7 Data gap-filling

Gaps in the EC flux time series (LE, H and NEE) were filled using the Marginal Distribution Sampling (MDS) method (Reichstein *et al.* 2005a). MDS is a variant of the mean diurnal variation (MDV) approach (Falge *et al.*, 2001) modified on the assumption that gap-filling is improved when the covariation of fluxes with meteorological conditions and the temporal autocorrelation of fluxes are considered (Reichstein *et al.*, 2005a; Papale *et al.*, 2006). Gap-filling was conducted using an online implementation of the Reichstein *et al.* (2005a) algorithm. Additional to the gap-filling of fluxes the tool also provides estimates for any missing records of R_g and T_{air} .

MDS fills gaps according to three methods depending on prognostic data availability (Reichstein *et al.*, 2005a). In the first (best) method, only flux data are missing; gaps filled using the mean of values obtained at the same time of day and under similar meteorological conditions (where R_g , T_{air} and VPD are within $\pm 50 \text{ W m}^{-2}$, $\pm 2.5^{\circ}$ C and $\pm 5 \text{ hPa}$, respectively). In the second method, flux data and T_{air} and/or VPD are missing and gaps are filled using the mean of values during which R_g is $\pm 50 \text{ W m}^{-2}$. In the third (least reliable) case, flux and prognostic data are missing. Short gaps (<0.5 days) are filled by linear interpolation, whereas longer gaps are filled using MDV (Falge *et al.*, 2001). In all cases, the algorithm starts with ± 7 day window either side of the gap. If gaps cannot be filled, window size is incremented ± 7 days until gap-filling is achieved (Reichstein *et al.*, 2005a). The online tool provides a QC flag for each gap-filled datum (Table 4.5), an artificial gap scenario which can be used to assess gap-filling performance, and an estimate of uncertainty for each gap-filled value.

Table 4.5: Data gap-filling quality classification scheme. The scheme is according to the online implementation of the marginal distribution sampling method of Reichstein *et al.* (2005a). The qualify flags (1 to 3) are assigned on the basis of the gap-filling method used (see text) and the length of the averaging time window used. A is the highest quality gap-filling; B is considered acceptable; and C is considered dubious. Non-applicable categories are indicated by n/a. (table modified from http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/method.php).

Averaging time window (days)	Gap-filling method					
	1	2	3			
0.5	n/a	n/a	А			
to 2.5	n/a	n/a	В			
> 2.5	n/a	n/a	С			
7	А	А	n/a			
14	А	В	n/a			
> 28	В	С	n/a			
> 56	С	С	n/a			

In this study, gap-filling was performed using all measurements obtained over the complete study period at both sites. At WSF, gap-filling of the entire measurement period (i.e. 20^{th} March 2009 to 31^{st} December 2010) provided an estimate of CO₂ exchange during the long data gap between 31^{st} December 2009 and 20^{th} March 2010. However, gaps filled using MDS during this period are biased by flux values obtained either side of the long gap (i.e. higher values during spring). Clearly, determination of an annual CO₂ balance requires measurements obtained over the cold winter period. Gap-filled estimates for this period are not presented here. For BF, gap-filling the full dataset provided a continuous record of NEE for 2010.

MDS gap-filling is best performed when complete meteorological records are available. Here, R_g , T_{air} and RH (for calculating VPD) gaps were filled prior to gap-filling of fluxes. At WSF, the AWS provided a continuous record of T_{air} and RH. All data analyses were based on these records (as they are measured at the standard meteorological measurement height of 2 m and showed good agreement with sensors on the EC tower) and no gap-filling was required. At BF, gaps in T_{air} and RH were only encountered during cold winter periods, and filled directly using WSF AWS measurements. For periods when both towers were operational, gaps in R_g were filled directly using data from the alternate tower.

In April 2009 a complete system failure led to the loss of all data over a ~12 day period at WSF (Table 4.4). R_g gaps for this period were filled using the online algorithm prior to gap-filling. It is acknowledged that this approach likely introduced additional error for this period; however, as records of T_{air} and VPD were available for this period, and as T_{air} is typically well correlated with R_g (and VPD with T_{air}), this approach was selected over the alternative of filling gaps according to category C. This source of error is accounted for in the uncertainty assessment described in Chapter 7 (but was found to be small – see Table 7.4). Any other short gaps in R_g (typically of less than a few hours and at night) were filled the same way.

4.7.1 Gap-filling evaluation

The performance of the NEE data gap-filling was assessed using the artificial data gap scenario provided by the online flux processing tool. Artificial data gaps totalling 10% of the original dataset (including real gaps) were introduced into the flux datasets; gap-filling was performed as above. Figure 4.9 shows scatter plots of measured versus gap-filled estimates of NEE provided by the gap-filling tool. Evaluation statistics derived from the artificial gap-filling of NEE are provided in Table 4.6 for WSF and BF.



Figure 4.9: Gap-filling evaluation for the Wicken Fen (left) and Bakers Fen (right) flux measurement sites. Gaps were filled using the marginal distribution sampling method (Reichstein *et al.*, 2005a). Scatter plots show gaps filled according to the categories provided in Table 4.5. Gap-filled NEE data are artificial gaps introduced by the online tool. Data are shown using units of g CO₂-C m⁻² for each thirty minute flux averaging interval. Note the different axis scaling.

MDS performed well for both sites (Figure 4.9 and Table 4.6). The majority of real data gaps for periods were filled according to categories A and B (Table 4.6). A greater number of artificial NEE gaps were filled according to category B at BF. Slopes close to unity (and small intercepts) indicate MDS was able to reasonably approximate measured NEE in the majority of cases, although a number of outliers were evident for both sites, as was a tendency towards higher scatter during daytime periods. Category A gap-filling slightly underestimated measured NEE at BF (slope of 0.98) although a 2% underestimation represents a small source of uncertainty in time-integrated estimates of NEE.

Table 4.6: Evaluation statistics for the gap-filling of net ecosystem CO_2 exchange at the Wicken Sedge Fen and Bakers Fen flux measurement sites. Gap-filling categories correspond to the values provided in Table 4.5. Where applicable, units are shown in g CO_2 -C m⁻² 0.5 hr⁻¹. Evaluation statistics for gap-filling class C at BF are omitted as only two artificial gaps were filled using this method.

	Wicken	Sedge Fe	n	В	akers Fer	1
Gap-filling category	Α	В	С	Α	В	С
Slope	1.00	1.02	1.30	0.98	1.00	2.14
Intercept	0.01	0.01	0.00	-0.003	-0.01	0.04
r ²	0.89	0.91	0.87	0.82	0.8	1
RMS	0.06	0.06	0.09	0.06	0.07	
Minimum error	-0.32	-0.19	-0.12	-0.41	-0.46	
Maximum error	0.55	0.34	0.07	0.46	0.23	
Mean error	0.00	0.00	0.00	0.00	0.00	
Mean absolute error	0.04	0.04	0.08	0.04	0.05	
Number of artificial gaps	3919	299	3	2567	427	2
Number of real gaps filled	11573	944	1	8301	820	3

4.8 Partitioning of net ecosystem exchange

Partitioning of NEE into GPP and ER was performed according to the adopted method of the FLUXNET community (Reichstein *et al.*, 2005a; Moffat *et al.*, 2007). Use of standardised procedures provides an important basis for between-site comparisons. Furthermore, the method was used in a recent multisite assessment of peatland CO_2 dynamics (Lund *et al.*, 2010). In this approach (Reichstein *et al.*, 2005a), a short-term exponential approach is used to model nocturnal ($R_g>20$ W m⁻²) NEE as a function of (air or soil) temperature. Nocturnal NEE data (representing ER only when photosynthesis is inactive) are used to parameterise the Lloyd & Taylor (1994) respiration model:

$$ER(T) = R_{10} exp\left[E_o\left(\frac{1}{T_{ref} - T_o} - \frac{1}{T - T_o}\right)\right]$$

$$4.4$$

where: R_{10} is basal ecosystem respiration at reference temperature (T_{ref}) of 10°C; E_o (K) is an activation energy (temperature sensitivity) parameter; and T_o is the temperature where ER reaches zero (set constant at -46.02°C to prevent over-parameterisation). The approach assumes model parameters are time-varying with changes in ecosystem properties (i.e. phenology, soil moisture, etc.). E_o is estimated using a fifteen-day (expandable) moving window; R_{10} estimated using a four-day (expandable) moving window; R₁₀ estimated using a four-day (expandable) moving daytime temperature measurements; GPP is estimated by difference (i.e. as GPP=|NEE-ER|).

 T_{air} was used as the driving variable in the flux partitioning as T_{peat} was unavailable for WSF and a complete T_{peat} record was not obtained at BF. Flux partitioning was performed using an online implementation of Reichstein *et al.* (2005a). A limitation of the flux partitioning is that it does not account for possible suppression of autotrophic respiration during daylight hours, which may lead to underestimates of GPP (Lloyd, 2006; Osborne *et al.*, 2010). However, this potential systematic bias is not widely considered by EC studies (Cai *et al.*, 2010), and was not possible to evaluate on the basis of available instrumentation.

4.9 Energy balance closure

EBC was evaluated by linear regression of the sum of the turbulent energy fluxes (LE+H) against independently measured available energy (R_{net} -G). At WSF, lack of soil physics measurements (Table 4.1) precluded assessment of heat storage in the peat layer above the HFP01-SC. The heat storage term was not added to the BF HFP01-SC measurements as this requires accurate measurements of θ_{peat} and the thermal properties of (degraded) peat (Campbell Scientific Ltd, 2012), neither of which were available for BF. Moreover, field observations indicated soil physics measurements obtained at the flux tower location were unlikely to be representative of the wider tower footprint, particularly during non-growing season periods when open water was present at the peat surface. On the basis of these limitations, G was calculated as the mean of HFP01-SC measurements for both sites (i.e. two and three HFP01-SC plates at WSF and BF, correspondingly).

EBC was evaluated using (i) thirty minute flux data and (ii) daily averages of the turbulent and available energy fluxes (Leuning *et al.*, 2012). At the thirty minute timescale, EBC was assessed using all available flux averaging periods with full data availability (i.e. complete records of LE and H, and R_{net} and G). For daily averages, only days with complete available energy records (i.e. all available R_{net} and G measurements) were used. To minimise the influence of data gap-filling, only days with more than 75% available EC energy flux data were used in the daily fits (i.e. >32 LE and >32 H measurements). Regressions were conducted using orthogonal least squares, assuming random measurement error in both dependent and independent variables. Daily averages were calculated using the 24 hour period commencing at midnight.

Figure 4.10 shows EBC for the WSF (top panels) and BF (lower panels) flux measurement sites using thirty minute data (left panels) and daily averages (right panels). At both sites, the thirty minute turbulent energy fluxes were well correlated with the available energy (r^2 of 0.96 and 0.92, correspondingly). Thirty minute closure was higher at WSF than at BF, the regression slopes and small intercepts indicating closure of 84% and 71%, respectively (top panels in Figure 4.10 and Table 4.7). At both sites, regressions indicate the sum of the turbulent fluxes was under- and overestimated during periods of high (i.e. summer daytime) and low (i.e. at night) available energy, correspondingly. This is most likely explained by an underestimation of G at these peatland sites, as heat flux plates are known to perform poorly in peat substrates (Harding & Lloyd, 2008; Laurila *et al.*, 2012), and as heat storage and changes in water temperature were neglected. The pattern was more evident at BF than at WSF.



Figure 4.10: Energy balance closure for the Wicken Sedge Fen (top panels) and Bakers Fen (lower panels) flux measurement sites. The left panels show energy balance closure evaluated using all available thirty minute flux measurements. Lower panels show energy balance closure evaluated using daily averages. Regression equations, coefficients of determination and the number of data points used in the fits are provided on the plots and in Table 4.7.

EBC improved at both sites when assessed using daily averages (lower panels in Figure 4.10 and Table 4.7). The slope of the regressions indicated closure was 90% at WSF, and 87% at BF, representing improvements of 7% and 16% over thirty minute values, respectively (the regression slope improved to 94% at WSF if the 75% turbulent energy criterion was not applied but did not change at BF). This finding is consistent with results from a multisite evaluation (Leuning *et al.*, 2012), which found EBC improved across a range of FLUXNET sites when evaluated using daily averages, suggesting the energy residual is partly explained by lags relating to heat storage in the air, vegetation

and soil below z_m (Leuning *et al.*, 2012). The lower level of closure at BF is most likely explained by the higher degree of footprint heterogeneity (i.e. areas of standing water, bare peat, plant community heterogeneity) relative to the more homogenous conditions present at the semi-natural fen.

Table 4.7: Summary of regression coefficients and goodness of fit values for energy balance closure evaluated at the Wicken Sedge Fen and Bakers Fen flux measurement sites using thirty minute flux data and daily averages.

Slope	Offset	r^2	n
0.84	8.16	0.96	14046
0.90	4.24	0.97	112
0.94	-4.93	0.96	437
0.71	4.05	0.92	7963
0.87	-2.40	0.96	74
0.87	-8.36	0.93	344
	Slope 0.84 0.90 0.94 0.71 0.87 0.87	Slope Offset 0.84 8.16 0.90 4.24 0.94 -4.93 0.71 4.05 0.87 -2.40 0.87 -8.36	Slope Offset r ² 0.84 8.16 0.96 0.90 4.24 0.97 0.94 -4.93 0.96 0.71 4.05 0.92 0.87 -2.40 0.96 0.87 -8.36 0.93

Notes: The >75% criteria indicates regressions conduced for days with more than 36 H flux data points and more than 75% LE data points. Daily regressions using all data were conducted for days with full records of available energy (R_{net} -G).

At both sites, EBC was within the 70 to 90% range of values reported for a range of ecosystem types, globally (Wilson *et al.*, 2002). Closure at WSF using both thirty minute data and daily averages was towards the higher end of this range, serving to indicate the high quality of the EC measurements. BF EBC was towards the lower end of the reported range when evaluated at the thirty-minute timescale, but comparable to or higher than published values for a range of wetland and other EC sites, globally (e.g. Wilson *et al.*, 2002; Veenendaal *et al.*, 2007; Merbold *et al.*, 2009). Moreover, EBC improved significantly at BF when assessed using daily averages (Figure 4.10). On the

basis of the EBC assessment, and following current recommendations (Baldocchi, 2003; Foken *et al.*, 2011), no attempt was made to scale NEE measurements to the surface energy budget.

4.10 Chapter summary

This chapter has detailed the flux measurement sites, instrumentation and data handling protocols used in this research. An overview of the Wicken Fen National Nature Reserve and the Wicken Fen Vision was provided. The ecological and edaphic conditions at the study sites were described, together with the current land management practices employed.

The EC and all ancillary environmental instrumentation deployed at the two flux measurement sites were described. Details of all ancillary climatic and vegetation datasets used in the following results chapters were provided. EC flux data post-processing was conducted using standardised procedures using identical computation routines at both sites (with the exception of the angle-of-attack dependent correction to the WSF R3).

Site-specific QC protocols developed for this research were outlined. A summary of total NEE data coverage after QC procedures was provided. At both sites, total NEE data coverage was within the range of values attained at other EC measurement sites, globally, and comparable to that reported for other wetland environments.

Details of the methods used to fill gaps in the NEE time series and partitioning of NEE into GPP and ER were described. Assessment of the data filling technique indicated the

method performed satisfactorily in reproducing missing NEE flux values. The standardised method of the FLUXNET community was used to partition NEE into its component fluxes.

The plausibility of the EC flux measurements was evaluated by reconstructing the surface energy budget. EBC was higher at the semi-natural fen than for the regenerating site. Closure improved for both sites when daily averages were used in the analysis. EBC was within the range reported for other EC measurement sites, globally, and comparable to other wetland ecosystems.

Chapter 5: Environmental conditions

This chapter summarises the environmental conditions observed over the measurement period. As such, it forms the basis for the analysis and interpretation of CO_2 flux measurements presented in subsequent chapters. Monthly average air temperature and precipitation sums are presented and compared against longer-term meteorological observations. Water level measurements obtained at both sites are presented. Enhanced vegetation index (and leaf area index at BF in 2010) data are used to assess between-year and between-site differences in ecosystem phenology.

5.1 Meteorology

The East Anglian Fenland was characterised by strong seasonal variation in weather conditions during the measurement period (Figure 5.1). Significant between-year differences and departures from long-term (1979 to 2008) averages were observed for a number of months. Figure 5.1 shows key monthly meteorological variables for each month of the measurement period. Where possible, monthly values observed during 2009 and 2010 are compared against 1979 to 2008 climate averages; monthly anomalies⁴¹ are also shown (left panels in Figure 5.2). A summary of monthly meteorological data measured at and/or near Wicken Fen is provided in Table 5.1. Monthly values obtained at the two Met Office stations showed good overall correspondence with monthly data from Wicken Fen⁴²; for consistency, all comparisons

⁴¹ Anomalies were calculated by subtracting the monthly 1979 to 2008 averages from the monthly values observed in 2009 and 2010.

⁴² Differences in air temperature measurements between Cambridge NIAB and Wicken Fen are due to geographical and urban/rural effects. As noted in Chapter 4, these data are considered sufficient for comparing the conditions of the measurement period against long-term temperature conditions.

against long-term averages are based on monthly values obtained at the same locations. Where relevant, monthly values measured at WF are given in parentheses.



Figure 5.1: Comparison of seasonal change in monthly meteorological variables measured in the East Anglian Fens during 2009 and 2010 (right panels). Thirty year normals are for the period 1979 to 2008. Monthly anomalies are shown on the left panels.

5.1.1 Global radiation

 R_g showed a symmetrical seasonal pattern in both years (top panel in Figure 5.1). Monthly R_g increased from low monthly totals at the start of the year, peaked during the summer months, and declined throughout autumn. Minimum monthly R_g was observed during December in 2009 and 2010. Maximum monthly R_g occurred during June in both years, and was slightly higher in 2010. Total monthly R_g was lower during April 2009, but higher during August and September of 2009 than for the corresponding months of 2010, respectively. April values are not directly comparable as R_g records for a number of days in this month of 2009 were gap-filled (Chapter 4), but lower values are consistent with differences in total hours of sunshine duration measured at Cambridge NIAB (161 and 212 hours, respectively). Lower R_g in August and September 2010 was coincident with extremely high late summer rainfall (discussed below). Total time-integrated R_g was higher during the summer (June, July and August) and main growing season (May to October) of 2009 than for the same intervals of 2010 (Table 5.1), mainly due to low total monthly R_g in August 2010.

Table 5.1 (next page): Summary of meteorological variables observed during 2009 and 2010. Global radiation data were measured at Wicken Fen. Monthly air temperature and precipitation data measured at Wicken Fen are compared with data obtained at UK Met Office sites in Cambridge and Stetham, respectively. Mann-Whitney U tests indicate air monthly air temperature values marked with an * were found to be statistically greater at the 95% confidence level than for the corresponding time period of the other measurement year.

	Global radiat	ion (M W m ⁻²)		Air tempera	ature (°	°C)		Ai	r frost	(days)		Precipit	ation (1	mm)	
Month	Wick	en Fen	Wicke	en Fen	Ca	mbridg	e NIAB	Car	nbridge	e NIAB	Bake	rs Fen		Stretha	ım
	2009	2010	2009	2010	2009	2010	79 to 08	2009	2010	79 to 08	2009	2010	2009	2010	79 to 08
January		41.0	2.5 (3.6)*	1.1 (3.0)	3	1.8	4.4 (2)	13	15	10 (6)		43	35	44	46 (21)
February		65.6	3.8 (3.9)*	2.5 (2.8)	4.5	3.3	4.4 (2.2)	13	12	10 (6)		73.8	46	65	32 (17)
March		156.4	6.5 (3.9)*	6.1 (4.6)	7.4	6.9	6.7 (1.4)	6	9	5 (4)		31	29	29	42(20)
April	222.9	268.3	10.1 (4.2)*	9.0 (4.7)	10.5	9.3	8.7 (1.1)	0	3	3 (2)		8.8	10	10	41 (29)
May	332.8	326.3	12.7 (4.2)*	10.9 (5.3)	13	11.2	12.0 (1.2)	0	2			38.6	25	30	50 (30)
June	339.4	340.2	14.8 (4.7)	15.1 (5.1)*	15.6	15.8	15.0 (1.0)	0	0			42.8	42	33	50 (32)
July	317.3	320.2	16.2 (3.9)	17.9 (4.1)*	17.3	19.2	17.4 (1.4)	0	0			36.4	71	33	48 (23)
August	288.4	229.1	17.1 (4.2)*	15.3 (3.6)	18.4	16.6	17.4 (1.3)	0	0			121.6	45	145	53 (28)
September	196.1	167.1	14.0 (4.1)*	13.4 (3.9)	15.3	14.8	14.8 (1.2)	0	0			75.8	10	58	46 (25)
October	105.0	108.4	10.9 (3.5)*	10.3 (4.2)	12	11.2	11.2 (1.5)	0	0	1 (2)		61	35	50	57 (26)
November	60.1	60.1	8.5 (3.3)*	4.9 (5.1)	9.3	5.7	7.2 (1.3)	0	9	4 (4)	94	28.8	84	33	51 (20)
December	43.2	37.2	2.9 (3.8)*	-0.4 (3.6)	3.4	0	5.0 (1.5)	12	23	9 (5)	51.6		65	23	46 (22)
JJA	945.1	889.5	16.1 (4.4)	16.1 (4.5)	17.1	17.2	16.6 (0.9)					201	158	211	150 (47)
May to Oct.	1579.0	1491.2	14.3 (4.61)*	13.8 (5.2)	15.3	14.8	14.6 (0.7)		2			376	228	349	304 (70)
Annual		2113.6	10.1 (6.4)*	8.9 (7.2)	10.8	9.6	10.4 (0.7)	44	73	42 (13)			497	552	560 (83)

5.1.2 Air temperature

Average monthly T_{air} closely followed the seasonal pattern in R_g (Figure 5.1). On an annual basis, 2009 was warmer than the long-term average (10.4°C) whereas 2010 was cooler (Table 5.1). Mean annual T_{air} was 10.8°C (10.1°C) and 9.6°C (8.9°C) in 2009 and 2010, respectively (Table 5.1). Results of a Mann-Whitney U test (using data from WF) confirm 2009 was statistically warmer than 2010 (p<0.05). Mann-Whitney U tests confirmed all months of 2009 were statistically warmer at WF than during 2010 (p<0.05), excluding June and July which were statistically warmer in 2010 than in 2009 (p<0.05). The May to October period was warmer in 2009 than during 2010 (p<0.05) with mean T_{air} of 15.3°C (14.3°C) and 14.8°C (13.8°C), correspondingly (Table 5.1).

The study period experienced some of the coldest winter conditions in recent decades. Conditions were colder than normal during all winter months except February 2010 (Figure 5.1; Table 5.1). All winter months experienced a higher than average number of frost days (Figure 5.1). December was the coldest month during both measurement periods (no flux data were available for January 2009) with monthly average T_{air} over one standard deviation (SD) cooler than normal (Figure 5.1; Table 5.1). December 2010 was the coldest month in the Fenland (and the UK more generally) for at least three decades. Mean T_{air} for this month was 0°C (-0.4°C), over 5°C lower (>3 SD cooler) than the thirty-year average and accompanied by an unprecedented (>3 SD higher than the thirty year average) number of frost days (Figure 5.1).

Spring (March, April and May) temperatures were warmer than average in 2009. April 2009 showed the largest spring T_{air} anomaly with a mean T_{air} almost 2°C higher (>1 SD) than the 1979 to 2008 average (Figure 5.1). No frost days were recorded beyond

April in 2009 (Table 5.1; Figure 5.1). In 2010, early spring T_{air} (March and April) were close to normal, although March experienced a higher than average frost days. May 2010 was cooler than average with mean T_{air} approximately 2°C cooler than that of the previous year and accompanied by two late season frost days (Figure 5.1).

Mean summer (average of June, July and August) T_{air} was similar during the two years at 17.1°C (16.1 and 16.2, respectively) (Table 5.1). Average T_{air} was similar during June in both years (at Cambridge NIAB), although WF data (Table 5.1) indicate June 2010 was statistically warmer than 2009 (p<0.05). The timing of the warmest month differed during 2009 and 2010. August was the warmest month of 2009 with an average T_{air} of 18.4 °C (17.1°C)⁴³ whereas July was close to the thirty-year average. In 2010, warm (and dry) conditions commenced towards the end of June and persisted throughout July. July 2010 was the warmest month of the measurement period with a mean T_{air} of 19.2 °C (17.9°C), almost 2°C warmer than the 1979 to 2008 average, whilst August 2010 was slightly cooler than average (consistent with lower R_g values and high rainfall during this month).

Considerable differences in autumn (September, October and November) T_{air} were observed during 2009 and 2010. Monthly T_{air} was warmer than average during all months of 2009. November 2009 was over 2°C (>1 SD) warmer than the thirty-year average (Table 5.1). In autumn 2010, mean monthly T_{air} was normal during September and October (Figure 5.1), whilst November was characterised by an early onset of cold conditions and a mean T_{air} more than 3°C cooler than during the preceding year.

⁴³ The air temperature difference between the monthly Cambridge NIAB and Wicken Fen temperature measurements is due to geographical and urban/rural influences.

Table 5.2: Thermal growing season length and accumulated degree days at Wicken Fen in 2009 and 2010. The thermal growing season length and accumulated growing degree days were calculated using mean daily air temperature measured at Wicken Sedge Fen. Accumulated growing degree days were calculated using a threshold base temperature of 5° C.

Year	Start of thermal growing season (date)	End of thermal growing season (date)	Length of thermal growing season (days)	Accumulated growing degree days (°C)	
2009	21 st February	10 th December	293	2092.5	
2010	13 th March	23 rd November	256	1870.1	

The observed between-year variations in T_{air} resulted in considerable differences in the length of the thermal growing season (TGS)⁴⁴ and accumulated growing degree days (AGDD)⁴⁵. In 2009, the TGS lasted 293 days, commencing on 21st February and ending on 10th December (Table 5.2). In 2010, cool spring conditions delayed the start of the TGS by 20 days relative to 2009 (Table 5.2). The earlier onset of cold conditions in late autumn reduced the TGS length by a further 17 days, a total difference of 37 days (Table 5.2).

Between-year differences in T_{air} are reflected in the annual pattern of AGDDs (Figure 5.2). The warmer conditions of early 2009 led to higher AGDDs relative to 2010. Warm

⁴⁴ The thermal growing season is the period of each year during which plants can grow. The start of the thermal growing season is defined as the first of five days with a mean daily temperature above 5°C. The end of the thermal growing season is the day preceding the first of five successive days with a mean daily temperature below 5°C (Department for Energy and Climate Change, 2011)

⁴⁵ Accumulated degree days were calculated using mean daily air temperature measured at Wicken Fen and a threshold base air temperature of 5° C.

conditions in July 2010 reduced the difference in AGDDs during this period, but relatively cool conditions for the remainder of the year resulted in increased divergence from August onwards (Figure 5.2). No further increase in AGDDs occurred after the end of the TGS in either year (Table 5.2). Total AGDDs were *circa* 2092°C and 1870°C for the two years, respectively, a net difference of 222°C (Table 5.2).



Figure 5.2: Comparison of accumulated growing degree days (AGDD) for 2009 and 2010 at Wicken Fen National Nature Reserve.

5.1.3 Precipitation

On an annual basis, 2009 was slightly drier than normal whereas 2010 was close to the 1979 to 2008 average (Table 5.1). Total annual P was within one SD of the thirty-year mean during both years, at 497 and 552 mm yr⁻¹ in 2009 and 2010, respectively (Table 5.1). However, large within- and between-year variation in the seasonal distribution of P was observed in 2009 and 2010 (Figure 5.1 and Figure 5.3). In both years, cool winter conditions resulted in a higher than normal amount of P falling as snow (not measured). P totals fell within one SD of the thirty-year average for all winter months of 2009, although December was wetter than normal. February 2010 was over one SD wetter than the long-term average, whereas December was over one SD drier (receiving 35% less P than December 2009). Both years experienced drier than average spring (and

early summer) conditions (Figure 5.1). April was the driest spring month in both 2009 and 2010, with both periods receiving only 10 mm rainfall (>1 SD below normal).

Considerable between-year differences in summer (June, July and August) and autumn (September, October and November) precipitation were observed in 2009 and 2010 (Figure 5.1). June was drier than average (but within one SD) during both years, with June 2009 slightly (27%) wetter than the following year. July was the wettest summer month of 2009 receiving 71 mm rainfall (equal to one SD above the long-term average for July), whereas July 2010 was drier (and warmer) than average. August 2010 was the wettest month of the measurement period and the second wettest month in the Fens in last three decades (after April 1998). Total P for this month was 145 (121.6) mm (> 3 SD above average) and accounted for over 26% of the 2010 P sum (Table 5.1). In 2009, September and October were drier than normal, with September receiving only 10 mm rainfall (>1 SD below normal). September and October were close to long-term average in 2010. November was (>1 SD above normal) wetter than average in 2009 and drier than average in 2010. In 2010, cool late autumn conditions resulted in one of the earliest snowfalls in the last three decades on 25th November.



Figure 5.3: Comparison of cumulative monthly precipitation during 2009 and 2010 against the 1979 to 2008 normal. Monthly precipitation data are from the Met Office station in Stretham. Data supplied by the Met Office.

The observed between-year differences in monthly P totals are illustrated using cumulative P plots in Figure 5.3. In both years, dry spring and early summer conditions resulted in accumulated P being lower than the thirty-year average from April through July. In 2009, dry conditions during late summer and autumn resulted in cumulative P remaining lower than the thirty-year average throughout the year despite higher than average rainfall during November and December (Figure 5.1; Table 5.1). In 2010, high August rainfall led to higher than normal accumulated P during late summer and autumn, thereby compensating for dry spring and early summer conditions in the annual sum.

5.2 Water levels

5.2.1 Wicken Sedge Fen

Between-year differences in meteorological conditions had a strong influence on water levels at WSF (Figure 5.4). Water levels were close to the fen surface at the start of the measurement period in both years (Figure 5.4). In 2009, water levels declined steadily between April and June, fluctuated around -50 cm during relatively wet conditions in July, before falling progressively during warm and dry conditions in early autumn. Water levels reached a seasonal minimum of -101.7 cm on 5th October 2009, before recovering steadily during wet conditions in November (Figure 5.1).

Water levels declined less rapidly during the cooler conditions of spring 2010. Rapid water level drawdown occurred following the onset of warm and dry conditions in late June, and water levels were lower between 29th June and 24th August than for the corresponding period of 2009. A seasonal water level minimum of -92 cm was observed on 26th July 2010. Rapid water level recovery occurred during wet conditions in August, when water levels increased by approximately 50 cm over the six day period between 22nd and 27th August (total P was 85.2 mm for this interval). Water levels remained significantly higher throughout autumn 2009 than during the respective period of 2010. Similar water levels were present at WSF by the start of December in both years.



Figure 5.4: Comparison of groundwater levels at Wicken Sedge Fen during 2009 and 2010. Data show the mean daily position of water levels relative to the fen surface. Values are the average of the two automated dipwells. Data supplied by the UK Environment Agency.

5.2.2 Bakers Fen

Water level measurements obtained using the three divers installed at BF are shown in the top left panel of Figure 5.5. Time traces from the three divers illustrate the spatial heterogeneity in hydrological conditions at BF. This supports the argument that soil physics measurements made within the tower compound are unlikely to be representative of conditions across the wider tower footprint, as well as using T_{air} in the flux partitioning (discussed in Chapter 4) and subsequent data analyses.

Diver one provides the longest record at BF and shows that water levels were higher during spring than in autumn and early winter (Figure 5.5). Diver three was installed at a wetter area of the site, and consequently captures a slower decline in spring water levels at this location. Diver two recorded water levels below the mean residual peat depth during the summer months; this most likely reflects incorrect insertion of the tubing, and the recording of water levels present within the tubing in the clay layer underlying the peat (Figure 5.5).



Figure 5.5: Groundwater levels and volumetric peat moisture content measured at Bakers Fen. Panel a shows the measurements from each of the three divers. Panel b shows the mean of the three divers (see main text for details). Volumetric peat moisture content is shown in panel c. All plots are daily averages.

Data from the three BF divers were averaged to provide a single estimate for BF (panel b in Figure 5.5). Measurements below one SD of the mean residual peat depth (i.e. -56 cm) were excluded prior to averaging. The limitations of this approach are acknowledged, particularly during the period of spring decline when the variance between the divers was greatest (panel b in Figure 5.5). However, given that all divers are located within the tower footprint, and in the absence of more spatially comprehensive information on water levels, this was considered to represent the best available estimate for BF. These data highlight the difficulties in monitoring wetland water levels at a limited number of point locations.

On the basis of the measurement limitations described above, average water levels at BF were close to (or above in some locations) the fen surface at the start of the 2010 growing season. Water levels declined during dry spring conditions and a water table was close to the peat base, or absent in drier locations (with shallower peat), during the summer months. Declining (relative) θ_{peat} content was observed after water levels reached minimal levels (Figure 5.5), indicating summer changes in θ_{peat} were largely independent of water table position at the tower location, and reflected the balance between growing season P and ET.

No significant rise in water levels was observed during the wet conditions in August, although the intense rainfall event in late August was registered by all three divers. A large increase in (relative) 5 and 30 cm θ_{peat} was observed at this time (lower right in Figure 5.5). This likely reflects a combination of initial runoff, followed by the rehydration of previously dry peat. No water was abstracted onto BF in 2010 due to site maintenance requirements (fencing repairs requiring plant access). Water level recovery from late summer onwards reflected the shift to a positive meteorological water balance (Figure 5.5).

5.3 Ecosystem phenology

Figure 5.6 shows fits of the seasonal change in MODIS EVI at WSF 2009 and 2010 and during 2010 at BF (using equation 4.1). Seasonal changes in growing season LAI at BF are also presented. At BF, LAI_{max} showed a close correspondence with the timing of EVI_{max} (Table 5.3), indicating the general efficacy of MODIS EVI as a means of assessing seasonal changes in the phenology of the two fens. As such, the following discussion is based primarily on seasonal changes in EVI.



Figure 5.6: Seasonal change in vegetation indices at the Wicken Sedge Fen and Bakers Fen flux measurement sites: (A) EVI for WSF in 2009 and 2010; (B) shows BF EVI for 2010; C shows a comparison of WSF and BF EVI for 2010; D shows BF LAI. Parameters for the fitted curves are provided in Table 5.3.

At WSF, EVI indicates an earlier greening during the warm spring of 2009 relative to the cooler conditions of spring 2010 (panel A in Figure 5.6). In 2010, EVI indicates a more rapid increase in vegetation activity relative to the previous year with the onset of warm conditions in late June and a higher seasonal maximum. The EVI fits indicate seasonal peaks of 0.55 and 0.63 (EVI_{max} in Table 4.3) on 11^{th} and 19^{th} August (JD_{max} in Table 5.3) at WSF, respectively, although overlapping 95% confidence intervals do not indicate the timing of EVI_{max} was statistically different during the two years (Table 5.3). EVI declined more rapidly from the (higher) seasonal peak in 2010 than in the previous year at WSF. EVI reached similar values by mid-November in both years (A in Figure 5.6).

Table 5.3: Model parameters (and 95% confidence intervals) and goodness of fit values for non-linear fits of equation 4.1 to MODIS enhanced vegetation index (EVI) and leaf area index (LAI) at Wicken Sedge Fen and Bakers Fen in 2009 and 2010. LAI data are only available for Bakers Fen.

	Wicken S	edge Fen	Bakers Fen			
	EVI 2009	EVI 2010	LAI 2010	EVI 2010		
Ενι (ΙΔΙ)	0.55 (0.03)	0.63 (0.05)	35(03)	0.64 (0.03)		
JD_{max}	223.4 (6.5)	231.5 (7.5)	216.1 (9.6)	215.6 (4.9)		
С	136.3 (13.2)	119 (12.8)	102.8 (19.7)	134.7 (8.5)		
r2	0.92	0.91	0.87	0.97		
RMS	0.03	0.05	0.24	0.03		

EVI data indicate an earlier greening of BF site relative to WSF in 2010 (panel C in Figure 5.6). At BF, an EVI_{max} of 0.64 (similar to the respective EVI_{max} value at WSF in 2010) occurred fifteen days earlier at BF than at WSF in 2010 (Table 5.3), and declined steadily from the seasonal maximum. The LAI fit indicates LAI_{max} (3.5 m⁻² m⁻²) occurred on a similar date to EVI_{max} (Table 5.3). EVI was similar at the two sites during the autumn period (panel C in Figure 5.6) although the fits indicate late season EVI was slightly higher at BF compared to WSF in 2010.

5.4 Chapter summary

This chapter has described and compared environmental conditions encountered during the 2009 and 2010 measurement periods. Considerable between-year differences in meteorological and hydrological conditions were observed for the two measurement years. Monthly air temperature and precipitation data were compared with longer term climatic patterns. Strong deviations from thirty year climatic averages were observed for some months of both years. Strong seasonal and between-site differences in hydrological and phenological conditions were observed for the two sites.

Mean annual temperature was warmer than the long-term average in 2009 whereas 2010 was cooler. Both years experienced cooler than average winter temperatures. 2009 was characterised by warmer than average spring and autumn conditions. 2010 experienced cooler than average conditions during late spring and an earlier onset of cold conditions in autumn, but the highest observed midsummer temperatures. Between-year differences in temperature resulted in a shorter thermal growing season in 2010 relative to the previous year and a reduced number of accumulated growing degree days.

Precipitation showed strong seasonal and between year variations in 2009 and 2010. 2009 was slightly drier than average whereas 2010 was close to the thirty year normal. Both years experienced drier than average spring and early summer conditions. July was the wettest summer month during 2009; August 2010 was the wettest month in the Fenland for the last three decades. Wet conditions during late summer in 2010 were associated with a significant reduction in irradiance relative to the same period of the previous year. In 2009, conditions were drier than average (and the corresponding period of 2010) during the late summer and early autumn period.

Seasonal differences in temperature and precipitation had a strong influence on water levels at both sites. At WSF, warm and dry conditions during late summer and autumn in 2009 resulted in maximal water level drawdown during the autumn period. In 2010, water levels reached minimum levels during midsummer, but recovered rapidly during August. At BF, water levels fell rapidly during dry spring conditions, and were close to (or at) the peat base during the summer months. The extreme late summer precipitation in 2010 resulted in an increase in (relative) soil moisture content at BF, but did not significantly influence water levels. No water was abstracted onto BF during autumn/winter 2010.

MODIS EVI indicated cool conditions in spring 2010 delayed the phenological development of the WSF vegetation relative to 2009. This delay was followed by greater vegetation activity during a warmer than average midsummer period in 2010. EVI indicated vegetation activity at BF was active earlier in the season than at WSF during 2010, with an earlier peak in maximum EVI.

Chapter 6: Seasonal change and factors influencing land/ atmosphere carbon dioxide exchange

This chapter analyses the seasonal pattern of thirty minute NEE at the semi-natural and regenerating former arable fens and explores the factors driving the measured CO_2 exchange. The first part of the chapter analyses seasonal changes in net ecosystem CO_2 exchange. The analysis initially focuses on between-year differences at the semi-natural fen in 2009 and 2010. Results from the regenerating fen for the complete cycle of 2010 are presented and compared against the semi-natural fen for the paired flux measurement period. An empirical modelling approach is used to analyse and compare the sensitivity of photosynthesis to key environmental drivers at the two fens. The final part of the chapter analyses and compares the main environmental factors influencing ecosystem respiration at the two peatlands.

6.1 Analysis methods

6.1.1 Analysis of seasonal variation

Seasonal variation in land/atmosphere CO_2 exchange were analysed on a monthly basis. Monthly mean diurnal patterns of NEE (and environmental variables) were calculated to compare between-year (WSF only) and between-site (WSF versus BF) differences in the seasonal pattern of NEE. Average diurnal variations were calculated using measured (not gap-filled) NEE data only. Monthly diurnal variations were calculated using thirtyminute NEE measurements (and corresponding environmental variables) obtained at the same time of day during each month. All fluxes in this chapter are presented in (the measured) units of μ mol CO₂ m⁻² s⁻¹. To aid comparison with the following chapters, values in the text are also provided in units of mg CO₂ m⁻² s⁻¹.

A light response model was used to analyse seasonal variations in photosynthetic and respiratory activity at the two fens. The model is a modified form of Michaelis-Menton equation that enables seasonal variations in photosynthesis and respiration rates to be compared at a standardised level of irradiance, irrespective of differences in other environmental conditions (Falge *et al.*, 2001; Carrara *et al.*, 2004). For each month of the measurement periods at WSF and BF, measured (not gap-filled) NEE data were used to parameterise an equation of the form:

$$NEE(PAR) = \frac{-\alpha PAR}{1 - (PAR/1500) + (\alpha PAR/GPP_{1500})} + R$$
6.1

where: PAR is photosynthetically active radiation (μ mol photons m⁻² s⁻¹); α (μ mol CO₂ μ mol photons⁻¹) is the apparent ecosystem quantum yield (or photochemical efficiency of photosynthesis); GPP₁₅₀₀ (μ mol CO₂ m⁻² s⁻¹) is the optimum level of photosynthesis at a PAR level of 1500 μ mol photons⁻¹; and R (μ mol CO₂ m⁻² s⁻¹) is the intercept, providing an estimate of average monthly ER.

As PAR was not measured at Wicken Fen until the instrumentation of the BF site, PAR was estimated using a linear relationship derived from the R_g channel of the WSF CNR1 and the BF Quantum sensor (Figure 6.1). For consistency, modelled PAR was used for all fits (at WSF in 2009 and 2010 and BF in 2010). The use of (modelled) PAR

(over R_g) as the predictor variable was an arbitrary choice; however, as PAR is approximately twice the magnitude of R_g , the use of PAR only alters monthly estimates of α (Lasslop *et al.*, 2008), and was selected to enable comparison with similar studies.



Figure 6.1: Relationship between global radiation and photosynthetically active radiation. Global radiation data were measured using the Wicken Sedge Fen CNR1 net radiometer; photosynthetically active radiation data were measured using the Bakers Fen Quantum Sensor. Data were obtained for the period 19th March to December 2010. The small offset reflects an offset in the CNR1 net radiometer during nocturnal periods.

All monthly NEE data (day and night) were used to fit equation 6.1. This resulted in better fits (higher r^2 values) than use of daytime data alone. It is noted that monthly fits will result in aggregation error; however, regressions over shorter periods resulted in poorer quality fits and unrealistic parameters for periods with low data availability. As such, monthly fits are presented as this scale of analysis is sufficient for meeting the relevant research questions, and allows parameters to be compared directly with monthly environmental data (Chapter 5). Attempts to fit monthly nocturnal NEE data the Lloyd & Taylor (1994) respiration model resulted in realistic parameter estimates (and well constrained 95% confidence intervals), but poor determination coefficients (typically less that 0.2, and sometimes negative). As such, the analysis focuses on estimates of average monthly ER (expressed using R). Monthly parameters were estimated using non-linear least-squares optimisation (Levenberg-Marquardt algorithm) with the Statistics Toolbox of Matlab version 7.9.0.529 R2009b (The MathWorks Inc., Natick, Massachusetts., US, Release 2009b).

6.1.3 Drivers of land/atmosphere CO₂ exchange

Gross primary production

Although not fully independent, the analysis of the main factors influencing GPP and ER were conducted separately. An empirical multi-variate, non-linear regression model was used to explore and compare the sensitivity of photosynthesis to key environmental controls at WSF and BF. The approach used was initially developed for use with chamber flux data, but performed well in diagnosing the response of (partitioned) GPP to environmental variation at the two fens. The model provides ecologically interpretable parameters and has been used to diagnose and compare the response of photosynthesis across a variety of peatland types (e.g. Tuittila *et al.*, 2004; Riutta *et al.*, 2007a; 2007b; Leppälä *et al.*, 2011).

GPP was modelled as a function of PAR, T_{air} and water levels. The response to PAR was modelled as saturating. In line with ecological theory, responses to T_{air} and water
levels were assumed Gaussian. Including the response to water levels improved fits for both sites. Inclusion of EVI did not significantly alter other parameter estimates at WSF, but resulted in unrealistic fits at the regenerating fen; as such, EVI was not included in the analysis.

Thirty minute (flux partitioned) estimates of GPP (Chapter 4) for the paired measurement periods of 2010 were used to parameterise a model, given by:

$$GPP(PAR, T_{air}, WL) = \frac{GPP_{opt} \cdot PAR}{k + PAR} \cdot exp\left(-0.5\left(\frac{T_{air} - T_{opt}}{T_{tol}}\right)^2\right)$$

$$exp\left(-0.5\left(\frac{WL - WL_{opt}}{WL_{tol}}\right)^2\right)$$

$$6.2$$

(after Strack & Zuback, 2012) where: GPP_{opt} is the maximum potential rate of photosynthesis when T_{air} and water levels are not limiting; *k* is the level of irradiance (PAR) at which photosynthesis attains 50% of its maximum rate (representing light use efficiency); T_{opt} and WL_{opt} are the optimal T_{air} and water level for photosynthesis; and T_{tol} and WL_{tol} are parameters describing the tolerance of GPP to T_{air} and water levels, denoting the departure from optimal values where photosynthesis reaches 61% of its maximum rate (Riutta *et al.*, 2007a). Model performance was assessed by generating validation datasets, where one in every twenty GPP data points was removed prior to the optimisations. Fits were performed using non-linear least-squares regression with the Statistics Toolbox of Matlab version 7.9.0.529 R2009b (The MathWorks Inc., Natick, Massachusetts, US).

6.1.4 Ecosystem respiration

Daily averages of nocturnal ($R_g < 20 \text{ W m}^{-2}$) NEE were used to analyse the main environmental factors influencing ER. Nocturnal averages were selected over thirty minute flux values to minimise the influences of lags relating to CO₂ production within the soil profile and its measurement at the tower (Lloyd, 2006). Similar to Lafleur *et al.* (2005), average nocturnal ER values were retained for analysis for days when more than six high quality nocturnal NEE measurements were available. Daily averages of T_{air} and water levels (and relative θ_{peat} at BF) were also calculated for each period, and used to explore relationships with daily average nocturnal ER. The forms of the relationships between ER and environmental variables are described with the results presented below.

6.2 Seasonal change

6.2.1 Fingerprint plots

Fingerprint plots of (measured and gap-filled) NEE (and R_g and T_{air}) are presented in Figure 6.2 for WSF in 2009 and 2010 and BF in 2010. The plots illustrate the 'breathing' of the two fen ecosystems over the respective measurement periods. Colours towards the red end of the NEE scale illustrate periods of net CO₂ efflux (i.e. positive values at night and during ER dominated winter periods). Blues indicate periods of net CO₂ absorption during periods when photosynthetic assimilation outpaced respiratory losses (i.e. negative NEE values during daylight hours in the growing season).



Figure 6.2: Fingerprint plots of net ecosystem CO_2 exchange (top panels), global radiation (lower left) and air temperate (lower right) at Wicken Sedge Fen in 2009 and 2010 (top left) and at Bakers Fen in 2010 (top right). NEE plots are measured and gap-filled values produced using the online version of the Marginal Distribution Sampling method (Reichstein *et al.*, 2005a). NEE units are µmol CO_2 m⁻² s⁻¹; global radiation (R_g) and air temperature (T_{air}) are shown in W m⁻² and °C, respectively. Months are represented by increases along the ordinate; time of day is indicated along the abscissa. White space represents periods when no flux data were available. Note different scaling on the NEE colour bars for the two sites.

At both sites (both years at WSF) the seasonal pattern of NEE showed close correspondence with the radiation and temperature regimes (Figure 6.2). The width of the daily uptake period was closely associated with changes in day length, whereas the magnitude of net daytime uptake closely corresponded with seasonal variation in

radiation intensity and T_{air} . Seasonal variations in the magnitude of nocturnal CO₂ loss were associated with changes in T_{air} . At WSF, the delayed onset of warm conditions and early arrival of cold winter conditions in 2010 relative to 2009 is evident, illustrated by lower nocturnal fluxes and a slower increase in daytime net CO₂ uptake during spring, and an earlier reduction in the magnitude of nocturnal CO₂ losses during autumn, respectively.

6.3 Mean diurnal patterns

Figure 6.3 compares monthly mean diurnal cycles of NEE and selected environmental variables for the respective measurement periods at the two fens. The plots show changes in the amplitude of the monthly diurnal cycles of NEE in response to phenological changes in assimilatory and respiratory activity and illustrate seasonal, between-year and between-site differences in the magnitude of NEE during these periods.

Only partial data coverage was obtained at WSF during March in both years and at both sites during late December 2010 (Table 4.3). Monthly averages for these periods reflect conditions under which measurements were obtained. In the former instance, these represent warmer conditions towards the end of March (and are therefore not directly comparable with more complete monthly data coverage at BF). In terms of the latter, the 2010 data (for both sites) are biased towards conditions during early December 2010 (Tables 4.3 and 4.4). Similar data coverage during December 2010 was considered adequate for a between-site comparison (when temperatures were at their coldest and CO_2 flux densities were low).

At both sites, and during both years at WSF, daily average NEE showed a clear diurnal pattern in all months (Figure 6.3). Similar to Figure 6.2, the diurnal cycle was characterised by periods of nocturnal CO_2 efflux, with NEE becoming progressively more negative (positive) in response to increases (decreases) in irradiance. Net CO_2 uptake (or less positive daytime NEE) during all months indicates photosynthesis was active at both sites throughout the respective measurement periods (Figure 6.2 and 6.3). PAR was the primary driver of the monthly average diurnal pattern of NEE (discussed below), with maximum rates of (monthly average) net CO_2 uptake occurring as (monthly average) irradiance peaked around solar noon. Seasonal changes in the magnitude of the nocturnal CO_2 efflux co-determined the amplitude of the monthly diurnal patterns.



Figure 6.3: Comparison of monthly mean diurnal cycles of net ecosystem CO_2 exchange at Wicken Sedge Fen for 2009 and 2010 (top) and Wicken Sedge Fen and Bakers Fen for 2010 (second from top). Average diurnal cycles of key meteorological variables are also provided. The lower panel shows mean water levels relative to the fen surface. Meteorological variables represented by green lines represent data for 2010. WSF data for March represent the period 20^{th} to 31^{st} March only. Standard errors have been omitted to improve readability.

Large between-year variations in the average diurnal cycles of NEE were observed for (some months of) 2009 and 2010 at WSF (Figure 6.3). Estimates of maximum monthly average ($\pm 95\%$ confidence interval) net CO₂ uptake showed a clear seasonal trend, ranging from -0.51 \pm 0.16 to -20.39 \pm 0.89 µmol CO₂ m⁻² s⁻¹ (-0.22 \pm 0.007 to -0.9 \pm 0.04 mg CO₂ m⁻² s⁻¹) in 2009 and from -1.46 \pm 0.43 to -18.43 \pm 0.73 µmol CO₂ m⁻² s⁻¹ (-0.06 \pm 0.02 to -0.81 \pm 0.03 mg CO₂ m⁻² s⁻¹) in 2010 (Figure 6.3). Maximum net uptake rates were higher than values (range: -4 to -11.5 µmol CO₂ m⁻² s⁻¹ or -0.18 to -0.51 mg CO₂ m⁻² s⁻¹) from boreal peatlands (Humphreys *et al.*, 2006; Sagerfors *et al.*, 2008; Adkinson, Flanagan & Syed, 2011), but similar to (slightly higher than) the -18 µmol CO₂ m⁻² s⁻¹ (0.79 mg CO₂ m⁻² s⁻¹) reported for a Finnish Reed Canary Grass plantation with a large graminoid biomass (Shurpali *et al.*, 2009).

Net CO_2 uptake rates were higher (more negative) between April and June in 2009 relative to 2010, but weregenerally lower (more positive) from September onwards. The greatest average net CO_2 uptake rates were observed during June 2009, and in July of 2010. The highest monthly (average) net CO_2 absorption rates for the measurement period were observed in June 2009, whereas the lowest net uptake rates occurred in December of both years. Maximum average net CO_2 uptake was of similar magnitude in August, despite lower (average) PAR in 2010 (and similar rates of average nocturnal loss). The largest net difference in average daytime CO_2 uptake rates was observed in May.

Monthly average nocturnal ER⁴⁶ (mean of measured monthly values when $R_g < 20 \text{ W m}^{-2}$) ranged from 1.91±0.08 to 8.89±0.21 µmol CO₂ m⁻² s⁻¹ (0.08±0.0035 to 0.39±0.01 mg CO₂ m⁻² s⁻¹) and from 1.24±0.1 to 9.96±0.24 µmol CO₂ m⁻² s⁻¹ (0.05±0.0044 to 0.44±0.01 mg CO₂ m⁻² s⁻¹) in 2009 and 2010, correspondingly (Table 6.1). Maximum peak season nocturnal CO₂ effluxes were considerably higher than values (range: 1.59 to 4.55 µmol CO₂ m⁻² s⁻¹ or 0.07 to 0.2 mg CO₂ m⁻² s⁻¹) reported for northern fens (Sagerfors *et al.*, 2008 and references therein), reflecting the large biomass of this site (i.e. higher autotrophic respiration), as well as warmer temperatures and a larger seasonal variation in water levels at this temperate location (the drivers of nocturnal ER are discussed below).

Mean nocturnal CO₂ efflux rates were higher during all months⁴⁷ of 2009 than 2010 with the exception of June, when mean nocturnal respiratory fluxes were of similar magnitude, and July 2010 when the maximum rates of nocturnal CO₂ efflux were observed at WSF (Figure 6.3 and Table 6.1). This pattern is consistent with that of monthly average air temperature (Figure 5.1). The highest average nocturnal CO₂ loss rates were observed during July of both years.

In 2009, maximum average night-time CO_2 losses lagged the peak in net uptake by a month, whereas maximum average rates of net CO_2 uptake and efflux occurred concurrently in July 2010. Average monthly nocturnal ER was higher from September

 $^{^{46}}$ A lower monthly average of 1.31±0.05 $\mu mol~CO_2~m^{-2}~s^{-1}$ (0.06±0.0022 mg CO₂ m⁻² s⁻¹) was calculated using data for the latter part of March 2009 (e.g. 19th to 31st March). A higher mean value of 1.65±0.11 $\mu mol~CO_2~m^{-2}~s^{-1}$ (0.07±0.005 mg CO₂ m⁻² s⁻¹) was calculated for the corresponding period of 2010.

⁴⁷ Excluding March with only partial monthly data coverage in both years.

onwards in 2009 relative to 2010 (Figure 6.3 and Table 6.1), consistent with generally higher night-time air temperatures, particularly during November and December, and lower late season water levels in 2009 than for the corresponding months of 2010 (Figure 6.3). Between-year differences in the magnitude of average nocturnal CO_2 loss were greater during autumn than at any other time at WSF (Figure 6.3).

The BF site showed strong seasonal trends in monthly diurnal averages of NEE in 2010 (second top panel in Figure 6.3). Monthly average diurnal patterns showed notable differences (and some similarities) to WSF during the paired measurement interval. Maximum average CO₂ uptake varied from -0.74±0.58 to -16.0±0.64 µmol CO₂ m⁻² s⁻¹ (-0.033±0.026 to 0.70±0.028 mg CO₂ m⁻² s⁻¹) at BF in 2010. Maximum net uptake rates were slightly lower than the -17 µmol CO₂ m⁻² s⁻¹ and -17.2 µmol CO₂ m⁻² s⁻¹ (-0.75 and 0.76 mg CO₂ m⁻² s⁻¹) reported for managed grasslands on organic soils in Finland (Lohila *et al.*, 2004) and New Zealand, respectively (Nieveen *et al.*, 2005).

Similar to WSF, the lowest average net CO_2 absorption rates were observed during December at BF (Figure 6.3). Peak rates of average net uptake were greater during spring at BF (April and May). Net CO_2 absorption peaked in June 2010, a month earlier than at the semi-natural fen. Average rates of net CO_2 uptake were lower at the regenerating site than at WSF during summer (June, July and August). Maximum uptake rates declined at BF after the seasonal peak, although (maximum) average net CO_2 uptake showed an increase during September relative to the previous month (Figure 6.3). Average daytime CO_2 uptake rates were of similar magnitude at both fens during early autumn (September) and winter (December), but higher at BF during October and November.

Average nocturnal ER ranged from 0.74 ± 0.08 to $8.59\pm0.25 \ \mu\text{mol}\ \text{CO}_2\ \text{m}^{-2}\ \text{s}^{-1}$ (0.033 ± 0.004 to 0.38 ± 0.011 mg CO₂ m⁻² s⁻¹) at BF in 2010 (Table 6.2). Average nighttime CO₂ losses were lowest in January and February (at 0.72 ± 0.06 and $0.75\pm0.06 \ \mu\text{mol}\ \text{CO}_2\ \text{m}^{-2}\ \text{s}^{-1}$ or 0.032 ± 0.003 and 0.033 ± 0.003 mg CO₂ m⁻² s⁻¹, respectively). Maximum average nocturnal CO₂ efflux rates were similar to (but marginally higher than) the 8 $\mu\text{mol}\ \text{CO}_2\ \text{m}^{-2}\ \text{s}^{-1}$ (0.35 mg CO₂ m⁻² s⁻¹) reported for managed boreal and temperate grasslands on organic soils by Lohila *et al.*, (2004) and Nieveen *et al.* (2005), correspondingly, and lower than maximum values from WSF.

Mean nocturnal CO_2 losses at BF were greater during April and May than at WSF, but lower at the regenerating site between June and August. Similar to WSF, maximum rates of (average) nocturnal CO_2 efflux were observed in July at BF in 2010 (Figure 6.3 and Table 6.2), coincident with the highest nocturnal air temperatures, and lagging the seasonal peak in net uptake by a month. Average night-time ER was higher at BF than at WSF during September and November, whereas estimates of monthly average nocturnal CO_2 efflux were similar at the two fens during October and December (Figure 6.3 and Table 6.2).

6.4 Seasonal trends in light use and respiratory parameters

6.4.1 Wicken Sedge Fen in 2009 and 2010

Figure 6.4 shows the response of daytime NEE to increasing levels of irradiance (PAR) for each month of 2009 and 2010 at WSF. Equation 6.1 performed well in describing the monthly variation in NEE at WSF. Determination coefficients (r^2) indicate the light-response function was able to explain between 53% and 92%, and 43% and 94% of the monthly variation in NEE during 2009 and 2010, correspondingly (Table 6.1). The quality of the fits was highest during the main growing period (April to October), with minimum r^2 values of 0.7 and 0.72 in 2009 and 2010, respectively (Table 6.1).

Similar to the mean diurnal cycles (top panel in Figure 6.3), net CO_2 uptake was notably higher during the warm spring and early summer at WSF in 2009 at similar levels of irradiance relative to corresponding periods in 2010. The pattern was reversed from July onwards, when net CO_2 absorption rates were generally higher in 2010 than for the respective months of the preceding year. The largest differences in the daytime light responses were observed for May and September (Figure 6.4).



Figure 6.4: Response of daytime net ecosystem CO_2 exchange to increasing levels of irradiance at Wicken Sedge Fen for each month of 2009 and 2010. Fitted curves show non-linear fits of equation 6.1. Parameters for the non-linear regressions and goodness of fit statistics are provided in Table 6.1. Seasonal trends in the parameter estimates are presented graphically in Figure 6.7.

Table 6.1: Monthly parameter estimates (and 95% confidence intervals) for non-linear fits of equation 6.1 to monthly net ecosystem CO_2 exchange data at Wicken Sedge Fen for 2009 and 2010.

	Wicken Sedge Fen 2009					Wicken Sedge Fen 2010					
	α	GPP ₁₅₀₀	R	Mean nocturnal NEE	r ²	α	GPP ₁₅₀₀	R	mean nocturnal ER	r ²	
March	0.006 (0.002)	5.35 (0.63)	1.34 (0.14)	1.31 (0.10)	0.85	0.007 (0.003)	6.07 (1.47)	1.72 (0.27)	1.65 (0.22)	0.55	
April	0.017 (0.002)	10.00 (0.30)	2.23 (0.16)	2.24 (0.11)	0.88	0.01 (0.001)	6.89 (0.23)	1.69 (0.14)	1.67 (0.12)	0.87	
May	0.032 (0.002)	17.84 (0.36)	4.13 (0.22)	4.05 (0.13)	0.91	0.024 (0.003)	12.19 (0.42)	2.93 (0.30)	2.89 (0.19)	0.78	
June	0.054 (0.004)	27.74 (0.56)	7.00 (0.40)	6.68 (0.23)	0.91	0.056 (0.008)	23.77 (0.92)	6.99 (0.76)	6.66 (0.47)	0.76	
July	0.049 (0.004)	28.68 (0.60)	9.21 (0.35)	8.89 (0.21)	0.92	0.061 (0.004)	30.46 (0.52)	10.31 (0.34)	9.96 (0.24)	0.94	
August	0.044 (0.004)	22.59 (0.60)	8.63 (0.34)	8.49 (0.26)	0.89	0.051 (0.004)	22.76 (0.53)	8.37 (0.25)	8.19 (0.23)	0.92	
September	0.043 (0.006)	15.48 (0.63)	7.30 (0.28)	7.18 (0.25)	0.85	0.037 (0.003)	18.86 (0.57)	5.84 (0.20)	5.74 (0.17)	0.91	
October	0.031 (0.005)	14.56 (1.32)	5.99 (0.25)	5.98 (0.17)	0.70	0.035 (0.005)	10.62 (0.64)	4.06 (0.17)	3.99 (0.17)	0.72	
November	0.018 (0.004)	7.78 (1.24)	3.83 (0.12)	3.84 (0.11)	0.57	0.025 (0.006)	5.33 (0.64)	2.17 (0.10)	2.15 (0.10)	0.62	
December	0.019 (0.006)	3.06 (0.48)	1.93 (0.08)	1.91 (0.08)	0.53	0.021 (0.010)	2.52 (0.58)	1.27 (0.10)	1.24 (0.10)	0.43	

Notes: α (µmol CO₂ µmol photons m⁻² s⁻¹) is the ecosystem quantum yield (initial slope of the light response curve); GPP₁₅₀₀ (µmol CO₂ m⁻² s⁻¹) is gross primary productivity at a PAR level of 1500 µmol photons m⁻² s⁻¹; R (µmol CO₂ m⁻² s⁻¹) is an estimate of average ecosystem respiration for each month; mean nocturnal ER (µmol CO₂ m⁻² s⁻¹) is the average of all high quality nocturnal NEE (ER) measurements for each month; r² is the determination coefficient.

Table 6.2: Monthly parameter estimates for non-linear fits of equation 6.1 to monthly net ecosystem CO_2 exchange data at Wicken Sedge Fen and Bakers Fen in 2010. Values for Wicken Sedge Fen are the same as in Table 6.1 but are reproduced for comparison. Monthly average nocturnal NEE data are provided for comparison.

	Wicken Sedge Fen 2010					Bakers Fen 2010					
	α	GPP ₁₅₀₀	R	Mean nocturnal ER	r ²		α	GPP ₁₅₀₀	R	mean nocturnal ER	r ²
January							0.012 (0.005)	2.19 (0.43)	0.74 (0.08)	0.72 (0.06)	0.60
February							0.008 (0.003)	2.11 (0.35)	0.77 (0.08)	0.75 (0.06)	0.49
March	0.007 (0.003)	6.07 (1.47)	1.72 (0.27)	1.65 (0.22)	0.55		0.015 (0.006)	3.01 (0.35)	1.05 (0.18)	1.02 (0.1)	0.49
April	0.01 (0.001)	6.89 (0.23)	1.69 (0.14)	1.67 (0.12)	0.87		0.024 (0.004)	10.96 (0.43)	2.34 (0.25)	2.30 (0.14)	0.80
May	0.024 (0.003)	12.19 (0.42)	2.93 (0.30)	2.89 (0.19)	0.78		0.039 (0.004)	17.29 (0.47)	4.43 (0.36)	4.22 (0.29)	0.86
June	0.056 (0.008)	23.77 (0.92)	6.99 (0.76)	6.66 (0.47)	0.76		0.056 (0.006)	22.01 (0.64)	6.33 (0.48)	6.01 (0.34)	0.86
July	0.061 (0.004)	30.46 (0.52)	10.31 (0.34)	9.96 (0.24)	0.94		0.06 (0.005)	22.45 (0.52)	8.95 (0.35)	8.59 (0.25)	0.89
August	0.051 (0.004)	22.76 (0.53)	8.37 (0.25)	8.19 (0.23)	0.92		0.053 (0.006)	16.51 (0.52)	7.01 (0.28)	6.82 (0.23)	0.85
September	0.037 (0.003)	18.86 (0.57)	5.84 (0.20)	5.74 (0.17)	0.91		0.054 (0.005)	17.67 (0.56)	6.54 (0.24)	6.39 (0.22)	0.89
October	0.035 (0.005)	10.62 (0.64)	4.06 (0.17)	3.99 (0.17)	0.72		0.046 (0.004)	12.90 (0.50)	4.22 (0.13)	4.12 (0.12)	0.87
November	0.025 (0.006)	5.33 (0.64)	2.17 (0.10)	2.15 (0.10)	0.62		0.035 (0.007)	8.07 (0.91)	2.82 (0.13)	2.75 (0.13)	0.67
December	0.021 (0.010)	2.52 (0.58)	1.27 (0.10)	1.24 (0.10)	0.43		0.017 (0.08)	2.11 (0.45)	1.15 (0.08)	1.13 (0.06)	0.53

Notes: α (µmol CO₂ µmol photons m⁻² s⁻¹) is the ecosystem quantum yield (initial slope of the light response curve); GPP₁₅₀₀ (µmol CO₂ m⁻² s⁻¹) is gross primary productivity at a PAR level of 1500 µmol photons m⁻² s⁻¹; R (µmol CO₂ m⁻² s⁻¹) is an estimate of average ecosystem respiration for each month; mean nocturnal ER (µmol CO₂ m⁻² s⁻¹) is the average of all high quality nocturnal NEE (ER) measurements for each month; r² is the determination coefficient.

Monthly parameters estimated using equation 6.1 showed similar seasonal trends at WSF in 2009 and 2010 (between-year differences are discussed below). In both years, all three monthly parameters increased during spring, peaked during summer (typically in July), and declined throughout autumn (Figure 6.7). Estimates of α positively correlated with GPP₁₅₀₀ and R in both years; GPP₁₅₀₀ showed a strong positive correlation with R (panels A to C in Figure 6.5 and Table 6.3). High correlations between the photosynthetic and respiratory parameters are consistent with a strong dependence of autotrophic respiration on photosynthesis and heterotrophic decomposition of root exudates and plant litter (Humphreys *et al.*, 2006; Cai *et al.*, 2010).



Figure 6.5: Relationships between monthly parameter estimates for non-linear fits of equation 6.1 at Wicken Sedge Fen in 2009 and 2010 and at Bakers Fen in 2010. A shows the relationship between α and GPP₁₅₀₀; B shows the relationship between R and GPP₁₅₀₀; C shows the relationship between α and R; D shows the relationship between R and monthly average nocturnal net ecosystem CO₂ exchange. Error bars have been omitted to improve readability. Data are for the main growing season (March to October).

Monthly α values (±95% confidence intervals) ranged from 0.006±0.002 to 0.054±0.004 μ mol CO₂ m⁻² μ mol photons⁻¹ (0.00026±0.000088 to 0.0024±0.0018 mg CO₂ m⁻² μ mol photons⁻¹) and from 0.007±0.003 to 0.061±0.004 μ mol CO₂ m⁻² μ mol photons⁻¹ (0.00031±0.00013 to 0.0027±0.0018 mg CO₂ m⁻² μ mol photons⁻¹) in 2009 and 2010, respectively (Figure 6. 7 and Table 6.1). Minimum values were estimated for March in both years, whereas maximum values were obtained for June and July in 2009, and for July in

2010. Maximum α values were towards the higher end of peak season light conversion factors (range: 0.017 to 0.054 µmol CO₂ m⁻² µmol photons⁻¹ or 0.00075 to 0.0024 mg CO₂ m⁻² µmol photons⁻¹) reported for northern peatlands (Humphreys *et al.*, 2006), but within the range of monthly values (0.019 to 0.078 µmol CO₂ m⁻² µmol photons⁻¹ or 0.00084 to 0.0034 mg CO₂ m⁻² µmol photons⁻¹) estimated for temperate grasslands on peat (Veenendaal *et al.*, 2007). Monthly estimates of α for the growing season showed statistically significant (p<0.05) positive correlations with EVI and T_{air} in both years (Table 6.3). EVI and α showed a similar response to T_{air} (C and D in Figure 6.6), implying that temperature is the primary driver via its influence on ecosystem phenology and leaf development.

Table 6.3: Spearman's rank correlation (ρ) coefficients (and their p-values) for relationships between light-use and respiratory parameters and environmental variables for Wicken Sedge Fen in 2009 and 2010 and Bakers Fen in 2010. Correlations were calculated using one-tailed Spearman's ranked correlation coefficient tests.

		α	GPP ₁₅₀₀	R	EVI	T _{air}	WL	WL*
WSF 2009	α		0.89 (0.0007)	0.88 (0.0009)	0.81 (0.01)	0.90 (0.002)		
	GPP ₁₅₀₀ R			0.89 (0.0007) 	0.79 (0.01) 	0.90 (0.002) 0.93 (0.001)	-0.67 (0.04)	-0.94 (0.01)
WSF 2010	α GPP ₁₅₀₀		0.84 (0.002)	0.92 (0.00007) 0.92 (0.00007)	0.74 (0.002) 0.69 (0.03)	0.95 (0.006) 0.98 (0.002)	 0.02 (0.001)	
	α		0.93 (0.00)	0.90 (0.0007)	0.83 (0.008)	0.95 (0.006)	-0.95 (0.001)	-0.89 (0.02)
BF 2010	GPP ₁₅₀₀ R			0.96 (0.00)	0.69 (0.03)	0.90 (0.01) 0.98 (0.0001)	-0.90 (0.002)	-1.0 (0.0013)

Notes: WL* indicates correlations calculated using data for March to October representing the period of average monthly WL decline in 2009. Correlations marked with a * were not statistically significant at the 95% confidence level.



Figure 6.6: Relationships between monthly light use and respiration parameters and monthly environmental variables for the main growing season (March to October) at Wicken Sedge Fen in 2009 and 2010. A shows EVI against α ; B shows EVI against GPP₁₅₀₀; C shows T_{air} against EVI; D shows T_{air} against α ; E shows T_{air} against GPP₁₅₀₀; F shows T_{air} against R; and G shows water levels against R. The line in panel G shows the relationship between water levels and R for the period of initial water level decline.

GPP₁₅₀₀ ranged from 3.06 ± 0.48 to $28.68\pm0.60 \ \mu mol CO_2 \ m^{-2} \ s^{-1} (0.13\pm0.02 \ to \ 1.26\pm0.03 \ mg CO_2 \ m^{-2} \ s^{-1})$ in 2009 and 2.52 ± 0.58 to $30.46\pm0.52 \ \mu mol CO_2 \ m^{-2} \ s^{-1} (0.11\pm0.03 \ to \ 1.34\pm0.02 \ mg CO_2 \ m^{-2} \ s^{-1})$ in 2010 (Table 6.1). Maximum values were generally higher

than comparable⁴⁸ parameters (range: 7.08 to 25.5 μ mol CO₂ m⁻² s⁻¹ or 0.31 to 1.12 mg CO₂ m⁻² s⁻¹) reported for other northern peatland environments including treed sites (Humphreys *et al.*, 2006), but were similar to the 29.09±2.5 μ mol CO₂ m⁻² s⁻¹ (1.28± 0.11mg CO₂ m⁻² s⁻¹) reported for a *P. australis* wetland (on mineral soil) in China at a site with a similar mean annual temperature (8.6°C) and precipitation sum (631 mm yr⁻¹) (Zhou, Zhou & Jia, 2009). High peak season GPP₁₅₀₀ values at WSF are consistent with the large aboveground biomass (and presumably LAI) at the WSF site (Humphreys *et al.*, 2006), as well as the extreme-rich (pH) status of this fen (Lund *et al.*, 2010).

The lowest monthly GPP₁₅₀₀ values were estimated for December in both years, with maximum values estimated for July. The highest GPP₁₅₀₀ value for the measurement period was estimated for July 2010, coinciding with the highest average net CO₂ uptake in 2010, and despite relatively high (average) daytime VPD during this month (Figure 6.3). GPP₁₅₀₀ showed statistically significant correlations with EVI and T_{air} (p<0.05) in both growing seasons (Table 6.3 and Figure 6.6). The strongest correlations were identified with T_{air} in both years (Table 6.3). These results may indicate that leaf area development (indicated by EVI) controls α whereas temperature more strongly regulates maximum photosynthesis rates.

R ranged from 1.34 ± 0.14 to 9.21 ± 0.35 µmol CO₂ m⁻² s⁻¹ (0.06±0.01 to 0.41±0.02 mg CO₂ m⁻² s⁻¹) and from 1.27 ± 0.10 to 10.31 ± 0.34 µmol CO₂ m⁻² s⁻¹ (0.06±0.0044 to

⁴⁸ The light use function used in this study expresses maximum photosynthesis rates at a standardised PAR level of 1500 μ mol photons m⁻² s⁻¹. In most other studies, similar parameters provide estimates of light saturated photosynthesis rates at an infinite level of PAR. As such GPP₁₅₀₀ values reported here can be interpreted as slightly more conservative estimates.

 0.45 ± 0.015 mg CO₂ m⁻² s⁻¹) in 2009 and 2010, correspondingly (Table 6.1). Monthly estimates of R showed good agreement with monthly average nocturnal NEE (D in Figure 6.5 and Table 6.3), highlighting the efficacy of the light response function (equation 6.1) in estimating average monthly ER. Departures from the 1:1 line at higher values reflect the use of all NEE data in fitting equation 6.1 (i.e. due to the higher ER rates during warmer daytime conditions).

Monthly estimates of R showed strong positive correlations with T_{air} in 2009 (ρ =0.93; p<0.05) and 2010 (ρ =0.95; p<0.05), and were negatively correlated with declining water levels (Table 6.3). The response of R to declining water levels was approximately linear (Figure 6.6) in 2010 (ρ =-0.93; p<0.05). In 2009, R was strongly correlated with water levels between March and August (ρ =-0.93; p<0.05), but showed a weaker correlation along the full water level gradient (ρ =-0.67; p<0.05). Similar to GPP₁₅₀₀, minimum estimates of R were obtained for December of both years, with seasonal maxima during July (Figure 6.7 and Table 6.1).

Monthly parameter estimates obtained for WSF showed statistically significant differences (and some similarities) for 2009 and 2010 (Figure 6.7). All three parameters (α , GPP₁₅₀₀ and R) were statistically greater during the warm conditions (with higher EVI and lower water levels) of April and May 2009 relative to spring 2010, clearly reflecting the warmer conditions and earlier greening of the site in 2009 (Chapter 5). With the exception of July, estimates of α were not statistically different from late summer onwards at WSF (Figure 6.7 and Table 6.1), indicating between-year differences in NEE during these periods were driven primarily by differences in light-

saturated photosynthesis rates (expressed as GPP_{1500}) and respiratory activity (expressed by R). The highest α value in July 2010 occurred concurrently with maximum EVI (Figure 5.6), and is most likely explained by greater leaf production following the onset of warm conditions in late June.



Figure 6.7: Seasonal trends in monthly ecosystem light use and respiratory parameters (and 95% confidence intervals) at Wicken Sedge Fen during 2009 and 2010. Parameters were estimated by fitting equation 6.1 to monthly net ecosystem exchange data obtained at Wicken Sedge Fen during 2009 and 2010. Parameter values and goodness of fit statistics are provided in Table 6.1.

In July 2010 (when mean EVI, T_{air} and water level drawdown reached seasonal maxima), estimates of GPP₁₅₀₀ and R were both statistically greater than for the same month of 2009. The relative increase in GPP₁₅₀₀ over R resulted in (slightly) higher rates

of net CO_2 uptake at similar light levels during this month (Figure 6.4), suggesting that warm and dry conditions serve to enhance peak-season net CO_2 uptake rates at this site. With the exception of August (when GPP_{1500} and R were statistically similar) and September, estimates of GPP_{1500} were statistically greater during late summer and autumn of 2009 than for 2010 Figure 6.7 and Table 6.1). In September, the largest lateseason difference in the daytime light response of NEE was explained by statistically greater and lower estimates of GPP_{1500} and R in 2010, respectively. Generally more positive daytime NEE in autumn 2009 (October and November) reflected higher rates of (average) ER outpacing generally higher rates of GPP_{1500} relative to 2010 during warm and dry conditions, as further demonstrated by lower light compensation points⁴⁹ from September 2010 onwards (Figure 6.4).

6.4.2 Bakers Fen and Wicken Sedge Fen in 2010

Figure 6.8 shows the dependence of daytime NEE on increasing levels of irradiance for each month of 2010 at BF (and WSF for the paired measurement period). r^2 values indicate irradiance explained between 46% and 89% of the monthly diurnal variation in NEE at BF in 2010, and a minimum of 80% during the main (April to October) growing season (Table 6.2), indicating PAR was the primary control on the diurnal variation in growing season NEE.

Monthly light responses during the paired measurement interval (Figure 6.8) showed features similar to the average diurnal patterns of NEE (Figure 6.2). Net daytime uptake rates were higher at the regenerating fen during the spring (April and May) and late

 $^{^{49}}$ The level of irradiance at which net ecosystem CO₂ exchange reaches zero

autumn (October and November) at similar light levels, whereas the opposite pattern was observed during the summer period. The largest between-site difference in the light response of NEE was evident for July (Figure 6.8), when higher rates of ER at WSF (relative to BF) were outpaced by even higher rates of photosynthesis.



Figure 6.8: Dependence of daytime net ecosystem CO_2 exchange to increasing levels of irradiance at Wicken Sedge Fen and Bakers Fen for each month of 2010. Wicken Sedge Fen data are the same as shown in Figure 6.3 but are reproduced to enable comparison. No data were available for the Wicken Sedge Fen for January and February. Fitted curves show non-linear fits of equation 6.1. Parameters for the non-linear regressions and goodness of fit statistics are provided in Table 6.2. Model parameters are presented graphically in Figure 6.9.

Monthly parameter estimates (from equation 6.1) showed strong seasonal trends at BF (Figure 6.9). All three parameters (α , GPP₁₅₀₀ and R) increased during the spring,

reached an annual maximum during July, before showing a reduction throughout late summer and autumn (Figure 6.9). Similar to WSF, growing season (March to October) parameters showed strong positive correlations with one another (Figure 6.5 and Table 6.3). Strong correlations of α and GPP₁₅₀₀ with R (ρ =0.90 and 0.96, respectively, both p<0.05), highlight a strong relationship between assimilatory and respiratory activity at BF.



Figure 6.9: Comparison of seasonal trends in monthly light use and respiratory parameters (and 95% confidence intervals) estimated for Wicken Sedge Fen and Bakers Fen in 2010. Wicken Sedge Fen parameters are the same as shown in Figure 6.7. No data were available for Wicken Sedge Fen in January and February 2010. Parameters were estimated from non-linear fits of equation 6.1.Parameters and goodness of fit statistics are presented in Table 6.2.

Estimates of α (±95% confidence intervals) ranged from 0.008±0.003 to 0.06±0.005 μ mol CO₂ m⁻² μ mol photons⁻¹ (0.00035±0.00013 to 0.0026±0.00022 mg CO₂ m⁻² μ mol photons⁻¹) at BF in 2010 (Table 6.2). These estimates showed a similar range to the semi-natural fen (and other grasslands on organic soils), but with a markedly different seasonal pattern (Figure 6.9). Monthly α values were not statistically different during

the winter and early spring months (January to March, and December) or between June and October at BF (Figure 6.9 and Table 6.2).

All three parameters were statistically higher at the regenerating fen relative to WSF during spring (April and May⁵⁰). This is consistent with the earlier greening of the BF site (Figure 5.6) in 2010. α values were not statistically different at the two fens during summer months, but were statistically greater at BF for September and October (Figure 6.9 and Table 6.2). Monthly α values showed a stronger correlation and steeper response to mean EVI at BF compared to WSF, whereas the correlation with (Table 6.3) and response to T_{air} was lower (Figure 6.10). Similar to WSF, the response of α and EVI to T_{air} was similar at BF (C in Figure 6.10), illustrating the importance of the thermal regime on the seasonal development of plant biomass and associated light use characteristics.

GPP₁₅₀₀ ranged from 2.11±0.35 to 22.4±0.5 μ mol CO₂ m⁻² s⁻¹ (0.093±0.015 to 0.99±0.022 mg CO₂ m⁻² s⁻¹) at BF in 2010 (Table 6.2). These values are within the range (of similar) parameters reported for temperate grasslands on temperate organic soils, but within a narrower range than the values estimated for WSF. Veenendaal *et al.* (2007) for example, reported maximum photosynthesis rates (at infinite PAR) in the range 1.2 to 32.7 μ mol CO₂ m⁻² s⁻¹ (0.053 to 1.44 mg CO₂ m⁻² s⁻¹) for intensively and extensively managed (mown and grazed) grasslands on organic soils in the Netherlands.

⁵⁰ Estimates of GPP₁₅₀₀ and R were statistically greater for WSF than for BF during March, whereas α was not statistically different; however, as the data for March at WSF reflect conditions towards the end of the month, the comparison is restricted to months with comparable data coverage.

Estimates of GPP₁₅₀₀ were statistically similar during all winter months (January, February and December) at BF, but showed statistically significant monthly increases (relative to preceding months) between March and June, and decreases from July onwards (Figure 6.9 and Table 6.2). GPP₁₅₀₀ was statistically similar for June and July, but showed a statistically significant reduction in August. The GPP₁₅₀₀ estimate for August was statistically lower than that of September. This most likely reflects a late season recovery of the grasses at BF with the return of more favourable growing conditions (i.e. increased soil moisture) after the period of intense summer rainfall during August. A similar late season 'flush' in photosynthetic activity was reported for (northern) Canadian grassland (Flanagan *et al.*, 2002).

GPP₁₅₀₀ was significantly lower at BF than at WSF between June and August. The largest difference was estimated for July. Estimates of GPP₁₅₀₀ were statistically higher at BF during April and May, and between October and November, but similar at the two fens during December. GPP₁₅₀₀ was positively correlated with mean EVI (ρ =0.69, p<0.05) at BF (Table 6.3), but showed a higher correlation with T_{air} (ρ =0.90, p<0.05). The response (slope) of GPP₁₅₀₀ to mean EVI was similar at the two fens in 2010, but with higher values at WSF at similar EVI (B in Figure 6.10). GPP₁₅₀₀ was less strongly correlated with T_{air} (Table 6.3) and showed a lower increase with average T_{air} at BF than at WSF in 2010 (E in Figure 6.10).



Figure 6.10: Comparison of relationships between monthly light use and respiration parameters and monthly environmental variables for the main growing season (March to October) at Bakers Fen and Wicken Sedge Fen for 2010. A shows EVI against α ; B shows EVI against GPP₁₅₀₀; C shows T_{air} against EVI; D shows T_{air} against α ; E shows T_{air} against GPP1500; F shows T_{air} against R; and G shows water levels against R. Lines are only shown when relationships were best described by a linear fit.

R ranged from 0.74±0.08 to 8.96±0.35 μ mol CO₂ m⁻² s⁻¹ (0.03±0.0035 to 0.39±0.015 mg CO₂ m⁻² s⁻¹) at BF in 2010 with the lowest values estimated for January and February (Table 6.1). Similar to WSF, estimates of R for BF were similar to monthly maximum mean nocturnal efflux rates (Figure 6.5 and Table 6.2). As with GPP₁₅₀₀, monthly estimates of R were statistically greater (lower) during the period of seasonal increase

(decrease) during spring (autumn) months. Estimates of R were not statistically different for August and September at BF (Figure 6.9 and Table 6.2).

Monthly estimates of R were within a narrower range at BF compared to the seminatural fen (Figure 6.9 and Table 6.2). Monthly R values were statistically greater at BF than at WSF during spring, similar at both sites in June, but statistically greater at WSF during July and August. Similar to GPP₁₅₀₀, the largest between-site difference in R (and mean nocturnal NEE) was estimated for July, the relative increase in GPP₁₅₀₀ over R resulting in considerably higher net CO₂ absorption at WSF during this month (Figures 6.3 and 6.8). R was generally higher at the regenerating fen from September onwards (Figure 6.9 and Table 6.2); consistent with greater plant activity (i.e. higher autotrophic respiration rates) and generally lower water levels (Figure 6.3). R was only statistically different at the two sites during September and November.

Monthly R values showed a stronger positive correlation with mean T_{air} at BF (ρ =0.98, p<0.05) relative to WSF (Table 6.3), but a showed a steeper increase at the semi-natural fen (F in Figure 6.10). R was less strongly correlated with declining water levels during the main growing season at BF (ρ =-0.90, p<0.05) than at WSF (ρ =-0.93, p<0.05) in 2010, but showed an ideal statistical correlation (ρ =1.0, p<0.05) at BF during the period of initial (March to August) decline (Table 6.3).

6.5 Gross primary production

The photosynthesis model (equation 6.2) performed well in reproducing GPP values (estimated from the flux partitioning) for both sites in 2010 (Figure 6.11). The model was able to explain 92% and 93% of the observed variation in GPP at WSF and BF during the paired measurement period, respectively (Table 6.4). Comparison of modelled values against the validation dataset yielded slopes close to unity and small intercepts for both sites (Figure 6.11). The model was able to successfully reproduce estimates of GPP with little systematic bias, although there was a slight tendency towards increasing scatter at high GPP values for both fens (Figure 6.11).



Figure 6.11: Comparison of modelled and measured gross primary productivity for the Wicken Sedge Fen and Bakers Fen flux measurement sites. Partitioned GPP values are data points estimated from the flux partitioning that were not used to fit the photosynthesis model. Modelled GPP data are values predicted using equation 6.2 with the parameters provided in Table 6.4 and the respective environmental data for each validation data point. The 1:1 line shows the perfect linear relationship. The regression equations, coefficients of determination (r^2) and the number of validation data points used in the fits (n) are provided on each plot.

In Figure 6.12 (after Riutta *et al.*, 2007a), the response of modelled GPP has been recalculated to illustrate the response of photosynthesis to each variable, individually (see caption for details). The light response parameters of equation 6.2 (k and GPP_{opt})

can be (broadly) interpreted as seasonal averages of α and GPP_{opt} for the periods used to fit the model⁵¹. GPP_{opt} was significantly higher at the semi-natural site than at BF, with values of 47.94±0.92 and 36.82±0.73 µmol CO₂ m⁻² s⁻¹ (2.11±0.04 and 1.62±0.03 mg CO₂ m⁻² s⁻¹), respectively. Conversely, *k* values of 796.43±32.74 and 503.29±16.05 µmol photons⁻¹, correspondingly, indicate the regenerating fen was able to use PAR more effectively at low light levels.

Table 6.4: Parameter values ($\pm 95\%$ confidence intervals) and goodness of fit statistics estimated using the photosynthesis model for Wicken Sedge Fen and Bakers Fen. Gross primary production data for the paired measurement period (19^{th} March to 31^{st} December 2010) were used to fit the models.

Parameter	Wicken Sedge Fen	Bakers Fen				
GPP _{opt}	47.94 (0.92)	36.82 (0.73)				
k	796.43 (32.74)	503.29 (16.05)				
T _{opt}	22.83 (0.43)	28.65 (1.00)				
T _{tol}	14.55 (0.56)	18.08 (0.76)				
WL _{opt}	-65.53 (0.64)	-47.99 (0.54)				
WL _{tol}	46.56 (0.75)	29.20 (0.76)				
r^2	0.92	0.93				
RMS	2.22	1.99				
Ν	6688	6688				

Notes: GPP_{opt} (µmol CO₂ m⁻² s⁻¹) is the optimum level of photosynthesis when other factors are not limiting; *k* (µmol photons m⁻² s⁻¹) is the level of PAR at which half the light saturated rate of GPP is attained. T_{opt} (°C) and WL_{opt} (cm) are the optimum air temperature and water levels for photosynthesis; T_{tol} (°C) and WL_{tol} (cm) denote deviations from optimal values at which photosynthesis attains 61% of its maximum rate (modified from Riutta *et al.*, 2007a).

⁵¹ Higher GPP_{opt} values compared to the maximum monthly GPP_{1500} value is because the GPP_{opt} parameter represents the maximum rate of photosynthesis estimated for non-limiting environmental conditions.

The response of photosynthesis to temperature and water level variation differed at the two peatland sites (Figure 6.12 and Table 6.4). T_{opt} was estimated at 22.83±0.43°C at the semi-natural fen, and 28.65±1.0°C at the regenerating site, a difference of *circa* 5.8°C. The estimate for BF was close to the maximum observed T_{air} in 2010 (28.9°C). BF showed a broader tolerance to T_{air} than the semi-natural fen, with T_{tol} estimated at 18.08±0.76°C compared to 14.55±0.56°C for WSF. These estimates are similar (T_{opt} range: 22.8 to 29.3°C; T_{tol} range: 12.3 to 17.8.°C) to values reported for boreal fen communities with vascular plants (Riutta *et al.*, 2007a).

 WL_{opt} for photosynthesis was lower at WSF than for BF in 2010. WL_{opt} was predicted at -65.53±0.64 cm and -47.99±0.54 cm for the two sites, correspondingly (Table 6.4). These values are significantly lower than optimum values of -8.54 to -16.0 cm reported by Riutta *et al.* (2007a), and the -11cm cm reported by Sonnentag *et al.* (2010). The lower WL_{opt} for WSF and BF most likely reflect plant adaptations to the more extreme water level variation at the study sites relative to boreal sites (e.g. Riutta *et al.*, 2007a; Sonnentag *et al.*, 2010). At BF, WL_{opt} was close to the mean depth of the residual peat layer (*circa* 0.55 m). The narrower WL_{tol} for BF ($WL_{tol}=29.20\pm0.76$ cm), and a steeper initial increase in GPP with falling water levels (Figure 6.12) indicates photosynthesis was more tightly regulated by water levels at BF, whereas primary production was less sensitive to water level variation at WSF ($WL_{tol}=46.56\pm0.75$ cm).



Figure 6.12: Response of modelled photosynthesis to environmental drivers at Wicken Sedge Fen and Bakers Fen. In each panel (following Tuittila *et al.*, 2004; Riutta *et al.*, 2007a) only the variable of interest has been allowed to vary and all others are set constant. PAR was set to the maximum observed value (1936 μ mol photons m⁻² s⁻¹); temperature and water level values were set to the optimal and tolerance parameters given in Table 6.4. Green and magenta dots show model residuals and indicate the variability in GPP that was not explained by the model.

6.6 Response to atmospheric vapour pressure deficit

The model used to assess the sensitivity of GPP to environmental variation did not include a potential reduction of GPP (and therefore more positive daytime NEE) due to stomatal closure under elevated atmospheric VPD (Lloyd, 2006; Shurpali *et al.*, 2009). Although this is not likely to affect the results presented above due to the strong correlation between T_{air} and VPD (Jacobs *et al.*, 2007), the contrasting conditions of summer of 2009 and 2010 (Chapter 4 and Figure 6.2) presented an opportunity to explore a potential reduction in NEE to increasing atmospheric moisture demand (i.e. increasing VPD). The period 6th July to 22nd August was selected for the analysis due to strong between-year differences in water levels and VPD at WSF at this time (Figures 5.4 and 6.2), as it was predicted that VPD would have greater influence on NEE (via its influence on GPP) when water levels (and presumably soil water availability) were lower (e.g. Lloyd, 2006; Sonnentag *et al.*, 2010; Lohila *et al.*, 2011).

Figure 6.13 shows fits of equation 6.1 to measured data for these time periods. Plots of model residuals against T_{air} and VPD indicated a greater number of positive residuals (when the model predicted more negative NEE than measured values) at T_{air} and VPD above *circa* 22°C (slightly higher at BF) and 15 hPa, correspondingly (lower two rows in Figure 6.13). Above these thresholds, model residuals showed a tendency towards an increasing trend as T_{air} and VPD increased.


Figure 6.13: Light responses (top panels) and residual plots for Wicken Sedge Fen and Bakers Fen for the period 6^{th} July to 22^{nd} August in 2009 and 2010. Residuals show the variability not explained by the light response model (equation 6.1). Positive residuals are when the model underestimated measured values (i.e. predicting more negative than observed NEE); negatives are the reverse. Residual plots are shown for air temperature (T_{air}) and atmospheric vapour pressure defecit (VPD).

Figure 6.13 shows plots of NEE measured at high irradiance (PAR>1200 μ mol m⁻² s⁻¹) against T_{air} and VPD greater than 22°C and 15 hPa, respectively (following an approach similar to Shurpali *et al.*, 2009 and Lohila *et al.*, 2011). Note considerably more negative NEE during 2010 at WSF, as well as the lower number of data meeting the prescribed criteria in 2009. NEE showed a statistically significant positive correlation

with VPD at WSF in 2009 (ρ =0.67, p<0.05), although a stronger correlation with T_{air} was identified (Table 6.5 and Figure 6.14). This may suggest the reduction in NEE more strongly reflects temperature-driven increases and/or reductions in ER and GPP, respectively, rather than a stomatal response to increasing VPD.

No significant correlation was identified between T_{air} and NEE at WSF for 2010 (Table 6.5 and Figure 6.14), although a statistically significant (but weak) correlation was identified with increasing VPD (ρ =0.28 and 0.46, respectively). Similarly, no statistically significant relationship was identified between T_{air} and NEE at BF in 2010 (p>0.05), whereas a significant (but weak) negative correlation was identified for NEE and VPD (ρ =0.48, p<0.05). The results from both ecosystems in 2010 suggest the reduction in NEE likely reflects a stomatal-induced reduction in GPP in response to the dry site and atmospheric conditions during this period. In terms of WSF, this result supports the prediction that VPD is a more important control on NEE (via stomatal control on GPP) when site conditions are drier.

	Vapour pressu	ure deficit	Air te	Air temperature (C)		
	Р	р	ρ	Р		
WSF 2009	0.67	0.01	0.92	0.00		
WSF 2010	0.46	0.005	0.28	0.10		
BF 2010	0.48	0.003	0.26	0.12		

Table 6.5: Spearman's rank correlation (ρ) coefficients (and p-values) for relationships between net ecosystem CO₂ exchange and gross primary production and air temperature and vapour pressure deficit at Wicken Sedge Fen in 2009 and 2010 and Bakers Fen in 2010.

Notes: Correlation coefficients (ρ) were calculated for periods when PAR was greater than 1200 μ mol photons m⁻² s⁻¹; and T_{air} and VPD were greater than 22°C and 15 hPa, respectively. Relationships between these variables are shown in Figures 6.14.



Figure 6.14: Relationships between air temperature and atmospheric vapour pressure deficit at Wicken Sedge Fen in 2009 and 2010 and at Bakers Fen in 2010. Data are for the period 6^{th} July to 22^{nd} August in both years. Linear fits are only shown when statistically significant correlations were identified (see Table 6.5). The same axis scaling is used for comparison.

6.7 Nocturnal CO₂ exchange (ecosystem respiration)

Figure 6.15 shows partial responses of daily average nocturnal NEE (ER) to changes in T_{air} and water levels at WSF for 2009 and 2010. Mean noctural ER showed an exponential dependance on T_{air} (panels A and B of Figure 6.15). Non-linear fits of the Lloyd & Taylor (1994) model (equation 4.4) indicated T_{air} was able to explain 66% and 72% of the variation in night-time NEE in 2009 and 2010, respectively (Table 6.6). Comparrison of modelled versus predicted values yeilded slopes close to one (with high scatter), although the model underestimated ER at low T_{air} in 2010 (panels C and D in Figure 6.15).



Figure 6.15: Partial responses of mean nocturnal net ecosystem exchange (ecosystem respiration) to variations in air temperature at water levels at Wicken Sedge Fen in 2009 (black data points) and 2010 (green data points). A and C show air temperature responses for 2009 and 2010, respectively; B and D show comparrisons on modelled versus measured values; E and F show the water level responses for 2009 and 2010, correpondingly. Air temperater responses were fitted using all nocturnal periods with more than six available nighttime measurements. Water level responses are for the period March to November. Parameter for the fits are provided in Tables 6.6 and 6.7.

Basal ER (R_{10}) was estimated at 5.05±0.24 for 2009 and 4.58±0.28 µmol CO₂ m⁻² s⁻¹ in 2010 (0.22±0.011 and 0.20±0.012 mg CO₂ m⁻² s⁻¹, respectively). Estimates of E_0 were 356.98±40.89 and 394.45±44.70 K for 2009 and 2010, correspondingly. Depsite these between-year differences, 95% confidence intervals suggest estimates of R_{10} and E_0

were not statistically different between the two years (Table 6.6). R_{10} values were within the 0.74 to 5.11 µmol CO₂ m⁻² s⁻¹ (0.033 to 0.23 mg CO₂ m⁻² s⁻¹) range estmated for a managed fen in the Somerset Levels (Lloyd, 2006), and towards the higher end of the 0.5 to 5 µmol CO₂ m⁻² s⁻¹ (0.02 to 0.22 mg CO₂ m⁻² s⁻¹) range reported for boreal bogs and fens standardised to 12°C (Silova *et al.*, 1996).

Table 6.6: Parameters (\pm 95% confidence intervals) for non-linear fits fits of the Lloyd & Taylor (1994) respiration model to mean nocturnal net ecosystem CO₂ data for Wicken Sedge Fen in 2009 and 2010 and Bakers Fen in 2010.

	Wicken See	lge Fen	Bakers Fen			
	2009 (T _{air})	2010 (T _{air})	2010 (T _{air})	2010* (T _{air})		
R ₁₀	5.05 (0.24)	4.58 (0.28)	4.48 (0.20)	4.68 (0.22)		
Eo	356.98 (40.89)	394.45 (44.70)	361.41 (30.18)	327.07 (33.81)		
r^2	0.66	0.72	0.82	0.75		
RMS	0.87	0.89	0.95	1.01		
n	206	193	218	176		

Notes: R_{10} (µmol CO₂ m⁻² s⁻¹) is basal nocturnal net ecosystem exchange (ecosystem respiration) at a reference temperature of 10°C; E_0 (K) is activation energy. The coefficient of detemination (r²), root mean square (RMS) error and number of data points used in the fits (n) are provided. The BF column marked with a * contains values estimated for the period of paired flux measurements in 2010 (19th March onwards in 2010).

Average nocturnal NEE (ER) showed a clear relationship with declining water levels at WSF (panels E and F in Figure 6.15). In both years, the partial response to water level variation was best described by a Gaussian curve (of the same form as equation 4.1), which explained 81% and 80% of the variation in average nocturnal NEE, respectively. Mean nocturnal ER increased in a near-linear manner with falling water levels, although

this was more pronounced in 2010 (with less scatter), before showing a reduction as water levels declined futher.

In 2009, the Gaussian fit indicated average nocturnal CO₂ efflux peaked at 8.74 ± 0.31 µmol CO₂ m⁻² s⁻¹ (0.38±0.014 mg CO₂ m⁻² s⁻¹) at a water level of -61.91±0.31 cm, whereas predicted losses reached a maximum of 9.24±0.39 µmol CO₂ m⁻² s⁻¹ (0.41±0.017 mg CO₂ m⁻² s⁻¹) at -75.91±6.87 cm in 2010 (Table 6.7). The reduction in average nocturnal NEE (ER) at low water levels was more evident in 2009 than for 2010, reflecting differences in the seaonal timing of maximum water level drawdown (i.e. lower temperatures as well as reduced autotrophic contributions during the period of maximum water level drawdown in autumn 2009).

Table 6.7: Parameters for Gaussian fits describing the partial dependence of nocturnal net ecosystem exchange on water level variation at Wicken Sedge Fen in 2009 and 2010. The partial response of nocturnal net ecosystem exchange to water level variation is shown in panels E and F of Figure 6.15.

	2009	2010
ER_{max} (µmol CO ₂ m ⁻² s ⁻¹)	8.74 (0.31)	9.24 (0.39)
WL _{max} (cm)	-61.91(1.85)	-75.91 (6.87)
<i>c</i> (cm)	52.80 (2.99)	61.87 (8.05)
r^2	0.81	0.80
RMS	1.14	1.34
Ν	206	192

Notes: ER_{max} (µmol CO₂ m⁻² s⁻¹) is the maximum predicted value of nocturnal ER; WL_{max} (cm) is the water level at which ER_{max} is reached; and *c* (cm) is a parameter describing the width of the fitted curves.

To further explore the abiotic drivers of ER, the exponential temperature model was combined with a Guassian response to water level variation. Mean nocturnal NEE data were used to fit an equation, given by:

$$ER(T_{air}, WL) = R_{10} exp\left(E_o\left(\frac{1}{T_{ref} - T_0} - \frac{1}{T_{air} - T_0}\right)\right)$$

$$6.3$$

$$. exp\left(-0.5\left(\frac{WL - WL_{opt}}{WL_{tol}}\right)^2\right)$$

(modified from Riutta *et al.*, 2007a; 2007b) where: R_{10} (µmol CO₂ m⁻² s⁻¹) and E_o (K) were defined previously, but in this case represent basal respiration (at 10°C) and the temperaure sensitivity of ER when water levels are non-limiting; similar to equation 6.2, WL_{opt} is the optimum water level for ER; WL_{tol} describes the water level tolerance (the departure from T_{tol} where ER is 61% of its WL_{opt}). Fits were computed using non-linear least-squares regression with the Statistics Toolbox of Matlab version 7.9.0.529 R2009b (The MathWorks Inc., Natick, Massachusetts, US).

	2009	2010
$R_{10} \ (\mu mol \ CO_2 \ m^{-2} \ s^{-1})$	6.60 (0.31)	7.29 (0.45)
$E_{o}(K)$	226.23 (33.03)	183.18 (36.29)
WL _{opt} (cm)	-66.53 (3.57)	-72.42 (5.78)
WL _{tol} (cm)	49.54 (5.15)	47.67 (6.09)
r^2	0.82	0.88
RMS	0.63	0.59
Ν	206	193

Table 6.8: Parameters (\pm 95% confidence intervals) and goodness of fit statistics for non-linear fits fits of equation 6.3 to mean nocturnal net ecosystem exchange (ecosystem respiration) data measured at Wicken Sedge Fen in 2009 and 2010.

Notes: R_{10} (µmol CO₂ m⁻² s⁻¹) is basal nocturnal net ecosystem exchange (ecosystem respiration) at a reference temperature of 10°C; E_o (K) is activation energy (temperature sensitivity); WL_{opt} is the optimum water level for ecosystem respiration (cm); and WL_{tol} (cm) represents the deviation from the Wl_{opt} where ecosystem attains 61% of it maximum rate. The coefficient of detemination (r²), root mean square (RMS) error and number of data points used in the fits (n) are provided

Modelling ER as a function of T_{air} and water levels changed estimates of R_{10} and E_0 from when T_{air} alone was used as the predictor variable (Table 6.8). Notably, estimates of R_{10} increased, whereas E_0 declined. Further, the relative magnitude of the paramter estimates was reversed (Tables 6.6 and 6.8). However, similar to the partial T_{air} reponse (Figure 6.15 and Table 6.6), values of R_{10} and E_0 obtained from equation 5.3 were not statistically different between the two years.

Combining dependancies on T_{air} and water levels using equation 5.3 resulted in similar responses of ER (Figure 6.16). Estimates of WL_{opt} and WL_{tol} were not statistically

different for 2009 and 2010, at -66.53 \pm 3.57 and -72.43 \pm 5.78 cm, and 49.54 \pm 5.15 and 47.67 \pm 6.09 cm, correpsondingly (Table 6.8). The model was able to explain 82% and 88% of the variation in average nocturnal NEE for 2009 and 2010, respectively, representing 16% improvements over the model driven by T_{air} alone for both years (Tables 6.6 and 6.8; Figures 6.15 and 6.16). This highlights the need to include temperature and water levels when modelling ER at this site.



Figure 6.16: Recalculated values of modelled nocturnal net ecosystem esxchange (ecosystem respiration) for Wicken Sedge Fen in 2009 and 2010. Similar to Figure 6.12, values have been recalculated so only one driver was allowed to vary at a time. Air temperature was set to the mean value calculated for 2009 and 2010 (10.4° C). Water level parameters were set to the optimal values given in Table 6.8. The lower panels compare modelled versus measured values. 1:1 lines show the perfect linear relationship. Regression equations, determination coefficients (r^2) and the number of data points (n) are provided.

Figure 6.17 shows partial responses of mean nocturnal NEE (ER) to variations in T_{air} and mean water levels and (relative) peat moisture content at BF. Average nocturnal NEE showed a strong exponential relationship with T_{air} (A in Figure 6.17). T_{air} was able to account for 82% of the seasonal variation in nocturnal NEE (ER). Comparrison of predicted against measured values yielded a slope close to one (and small intercept). The model slightly underestimated ER at high temperatures (B in Figure 6.17), with a tendency towards greater scatter. R_{10} and E_0 were estimated at 4.48±0.20 µmol CO₂ m⁻² s⁻¹ (0.20±0.01 mg CO₂ m⁻² s⁻¹) and 361.41±30.18 K, respectively. These values are slightly higher but similar to (annual) parameter values of 3.35 ± 0.23 µmol CO₂ m⁻² s⁻¹ (0.15±0.01 mg CO₂ m⁻² s⁻¹) and 345±34 K reported in the study of Veenendall *et al.* (2007). R_{10} was within the range of values reported by Silova *et al.* (1996) and Lloyd (2006).



Figure 6.17: Drivers of mean nocturnal net ecosystem CO_2 exchange (representing ecosystem respiration only) at Bakers Fen. A shows the response of mean nocturnal ER to air temperature; B compares modelled and measured temperature responses; C and D show responses of mean nocturnal NEE to changes in daily mean water levels and volumetric peat moisture content during the growing season, correspondingly.

 R_{10} and E_o parameters estimated for the paired measurement period of 2010 (note a lower r² value for BF compared to the annual fit) were statistically similar for the two fens (Table 6.6). Despite this similarity, the fits indicate a tendancy towards higher respiration rates at low temperatures at BF, whereas a higher temperature sensitivity (E_o) resulted in slightly higher nocturnal efflux at warmer T_{air} at WSF (Figure 6.18). These results are consistent with the analysis of seaonal change (above), where respiration rates were higher at BF during cooler periods (i.e. spring and autumn), and higher at WSF during the warm summer months. The similar overall (i.e. seasonal) temperature response at these two markedly different ecosystems characterised by markedly different seasonal respiration rates (e.g. Figure 6.3 and Table 6.2) clearly

refelcts the influence of factors other than temperature (i.e. soil moisure levels, phenology, etc.). This further confirms the need for a short-term modelling approach approach when partitioning NEE into its component fluxes (e.g. Reichstein *et al.*, 2005a).



Figure 6.18: Comparison of the air temperature response of mean nocturnal net ecosystem exchange (ecosystem respiration) at Wicken Sedge Fen and Bakers Fen for the period 19^{th} March to December 2010. Lines are non-linear fits of the Lloyd & Taylor (1994) respiration model (equation 4.4). Determination coefficients (r²) are shown on the plot. Parameters describing the fits are provided in Table 6.6.

Mean nocturnal ER showed a statistically significant (p<0.05) but weak ($r^2=0.36$) relationship with declining water levels up to *circa* -55 cm (Figure 6.17). ER was more variable and generally higher in the narrow range beyond this depth, when water levels were close to/at the peat base. Similarly, nocturnal NEE (ER) showed a statistically significant (p<0.05) but weaker ($r^2=0.32$) linear relationship with volumetric peat moisture content (Figure 6.17), possibly reflecting the poor representativeness of the (relative) soil moisture measurements in relation to the wider tower footprint. It was not possible to model ER using combined responses to temperature and water levels/peat

moisture. However, r^2 values indicate temperature was the most important abiotic driver of ER at the regenerating fen under the conditions observed during 2010.

6.8 Chapter Summary

This chapter has presented an analysis of the seasonal pattern and factors influencing land/atmosphere CO₂ exchange at the WSF and BF sites. Fingerprint plots and monthly mean diurnal cycles were presented for WSF in 2009 and 2010 and for BF in 2010. A light response function was used to compare seasonal trends in monthly light use and respiratory characteristics. An empirical model was used to compare the sensitivity of GPP at WSF and BF to variations in environmental drivers using data from the paired measurement period of 2010. The response of daytime NEE to increasing VPD was explored. An analysis of response of nocturnal ER to variations in temperature and hydrological conditions was presented.

At both sites, CO_2 fluxes showed a strong seasonal pattern. Flux magnitudes increased from low values during the spring months, peaked during the summer period, and declined throughout autumn. On a monthly basis, irradiance was able to explain most of the variation in NEE. Monthly parameters from the light response function showed similar overall seasonal patterns, and were strongly correlated with each other. Estimates of α and GPP₁₅₀₀ correlated with EVI and T_{air}. Average monthly respiration rates correlated with temperature and water levels at both fens.

The contrasting environmental conditions of 2009 and 2010 had a strong influence on (30 minute) CO_2 exchange dynamics at WSF. Warmer than average spring conditions

and the earlier greening of the fen resulted in significantly higher photosynthetic (i.e. expressed by α and GPP₁₅₀₀) and respiratory activity (i.e. R) compared to 2010. The highest monthly parameter values were associated with warm and dry conditions in July 2010. Late season CO₂ efflux rates were significantly higher during the warm and dry conditions of 2009 relative to 2010. In 2009, the earlier phenological development of the ecosystem resulted in more negative CO₂ uptake rates during spring compared to 2010, and an earlier seasonal peak in daytime NEE. Net uptake rates were more positive during autumn 2009 than in 2010 due to higher rates of ER.

Comparison of WSF and BF under near-identical meteorological conditions revealed differences in the seasonal pattern of CO_2 exchange in 2010. The photosynthesis of the vegetation at the regenerating fen was active earlier and later in the season compared to WSF. ER showed a similar overall pattern. In contrast, maximum photosynthesis (i.e. GPP_{1500}) and respiration rates were significantly higher at WSF during the summer months. These differences in assimilatory and respiratory activity resulted in higher net uptake rates at BF during the spring and early autumn, whereas net uptake rates were significantly more negative at WSF throughout the summer period.

The photosynthesis model performed well in reproducing estimates of GPP. In line with the analysis of seasonal change, the WSF plant community had a higher maximum rate of photosynthesis, whereas the regenerating fen was able to utilise light more efficiently. The semi-natural fen had a lower thermal optimum for photosynthesis than BF and was more tightly constrained by the temperature regime. The vegetation at the regenerating fen had a shallower water level optimum for photosynthesis, and was more tightly coupled to hydrological variation than the WSF community. The analysis of the VPD response of NEE indicated CO_2 uptake was reduced during dry atmospheric and soil conditions at both fens. At WSF, NEE showed a stronger correlation with T_{air} in 2009, indicating the reduction in NEE was a function of temperature-driven reductions in GPP and/or increased ER. A stronger correlation with VPD compared to T_{air} in 2010 indicates VPD may become a more important control on NEE (via a stomatal reduction in GPP) when water (and presumably soil moisture) levels are lower.

Analysis of nocturnal CO_2 flux measurements indicated variations in temperature and hydrological conditions influenced respiration rates at both fens. ER showed an exponential response to temperature and a Gaussian response to water level variation at WSF. Combining these responses using an empirical model improved the diagnostic power of a model driven by temperature alone. Temperature was able to explain most of the variation in ER at the regenerating fen. The two fens showed similar temperature responses during the period of paired measurements in 2010. ER showed statistically significant but weak linear responses to water level and (relative) soil moisture variation. The highest nocturnal CO_2 efflux rates were associated with the warm and dry midsummer period of 2010 at both fens.

Chapter 7: Carbon dioxide budgets of semi-natural and regenerating fens

This chapter presents time-integrated CO₂ budgets for the Wicken Sedge Fen (WSF) and Bakers Fen (BF) flux measurement sites. The chapter begins by describing the procedure used to obtain time-integrated estimates of NEE and its component fluxes and details of the method used to quantify uncertainty in seasonal and annual (BF only) estimates of NEE. Seasonal changes in daily CO₂ budgets are presented and compared. The analysis initially focuses on seasonal and between-year differences in daily GPP, ER and NEE at the semi-natural fen in 2009 and 2010. Daily CO₂ budgets for the regenerating ex-arable fen are presented for 2010 and compared against those of the semi-natural fen for the paired measurement period. The final part of the chapter presents and compares CO₂ budgets at monthly, seasonal and annual (at BF only) timescales.

7.1 Integration and uncertainty assessment

Time-integrated estimates of NEE and its component fluxes were obtained by summing gap-filled and flux partitioned estimates of GPP, ER and NEE at daily, seasonal (for WSF and BF) and annual timescales (BF only). In this chapter, all CO₂ fluxes are presented in units of g CO₂-C m⁻² (i.e. in units of carbon). Units of g CO₂-C m⁻² (i.e. carbon) can be converted to units of g CO₂ m⁻² (i.e. gaseous CO₂) using a conversion factor of 3.67.

Uncertainty in time-integrated seasonal and annual estimates of NEE was assessed using methods similar to Elbers *et al.* (2011). This method accounts for (i) uncertainties due to random measurement error and flux computations, (ii) uncertainty introduced by the method used to discard outliers, (iii) uncertainty relating to *u** threshold selection, and (iv) uncertainty introduced by gap-filling. The method assumes uncertainties are normally distributed and independent, and accumulate in quadrature (Elbers *et al.*, 2011). Uncertainties relating to rejection of data of poor technical quality were not considered; although it is noted that removal of data during unfavourable meteorological conditions (i.e. during precipitation events) represents a further potential source of systematic bias (e.g. Lafleur *et al.*, 1997).

Random measurement error and uncertainty introduced by flux calculations was assessed by applying a fixed percentage value to time-integrated estimates of NEE. On the basis of a review of (the few) EC studies to report random measurement errors, Elbers *et al.* (2011) concluded random measurement errors and flux computation routines typically introduce an uncertainty of *circa* \pm 5% annual NEE, although this may also be applicable to shorter (i.e. seasonal) integration periods (Jacobs, personal communication). Here, a more conservative \pm 20% was applied as a full year of data was not available for WSF (i.e. as random measurement error increases with shorter integration times), and to account for potential calibration error (Appendix A). The same conservative \pm 20% estimate was applied to BF NEE (seasonal and annual).

Uncertainty associated with outlier detection was estimated using gap-filled NEE datasets generated after filtering using more and less conservative *z*-values of 4.5 and 7,

correspondingly (Papale *et al.*, 2006). Uncertainty was estimated as the SD of the three time-integrated datasets (i.e. including the original). A similar approach was used to assess uncertainty due to u^* threshold selection. Gap-filled NEE datasets were created by filtering NEE using u^* thresholds of 0.05 and 0.15 m s⁻¹. As with outlier detection, uncertainty resulting from u^* threshold selection was approximated as the SD of the three datasets (Elbers *et al.*, 2011). At WSF, uncertainty associated with gap-filling of R_g (see Chapter 4) was assessed as the difference between time-integrated NEE datasets generated using gap-filled and non-gap-filled R_g values (i.e. filling the twelve day data gap in April 2009 according to category C – see chapter 4).

Uncertainty introduced by gap-filling was assessed using the uncertainty assessment provided by the online algorithm of Reichstein *et al.* (2005a). Here, an uncertainty estimate for each gap-filled data point is calculated as the standard error of the (measured) values averaged to fill gaps. Uncertainty associated with data gap-filling was calculated as the difference between time-integrated NEE calculated with and without these estimates⁵². Total uncertainty (x_t) for seasonal and annual estimates of NEE was calculated in quadrature using the Pythagorean Theorem, using:

$$x_t = \sqrt{x_a^2 + x_b^2 + x_c^2 + x_d^2 + x_e^2}$$
7.1

Where: x_a denotes measurement error and flux calculation uncertainty; x_b is uncertainty due to outlier removal; x_c is uncertainty due to u^* threshold selection; x_d is uncertainty introduced by data gap-filling; and x_e is uncertainty relating to gap-filling of R_g prior to

⁵² The online tool provides column vectors of NEE calculated with and without uncertainties.

gap-filling of NEE (only applicable to WSF in 2009 as discussed in Chapter 3). Uncertainties in time-integrated estimates of GPP and ER were not evaluated and are presented as estimated by the online tool.

7.2 Seasonal trends in daily CO₂ budgets

7.2.1 Wicken Sedge Fen

Figure 7.1 shows the seasonal change in daily GPP, ER and NEE at WSF during 2009 and 2010. Daily values of key environmental variables are also provided (see Figure caption for details). WSF was characterised by strong seasonal trends in the magnitude of the daily CO₂ exchange components (Figure 7.1). Estimates of daily GPP, ER and NEE showed similar overall seasonal patterns during 2009 and 2010; however, and in line with the analysis of seasonal change (Chapter 6), significant between-year differences in the magnitude of the flux components were observed for the two measurement periods (Table 7.1). For comparison, monthly and seasonal averages of daily NEE, GPP and ER are provided in Table 7.1.



Figure 7.1: Seasonal change in daily carbon dioxide budgets and environmental variables at Wicken Sedge Fen in 2009 and 2010. Green and red bars show daily sums of gross primary production and ecosystem respiration, respectively; black bars are total daily net ecosystem CO_2 exchange. PAR is total daily photosynthetically active radiation (modelled using R_g ; see Figure 6.1); T_{air} is daily average air temperature; EVI is enhanced vegetation index; WL is the mean daily position of water levels relative to the fen surface; and P is daily precipitation. Daily precipitation totals for 2010 (black bars) to the left of the dotted vertical line were obtained from the Wicken Fen Visitor Centre and are shown to illustrate the timing of precipitation events⁵³.

⁵³ The rain gauge at the Wicken Fen Visitor Centre is located on the roof of a building and in a sheltered position. Data from this rain gauge did not show good agreement with monthly totals measured at Stretham or with the tipping bucket rain gauge used at Bakers Fen.

Estimates of daily GPP (green bars in Figure 7.1) showed a similar seasonal trend in both years at WSF. GPP increased from low daily values at the start of both periods, increased throughout spring and summer, and declined as the vegetation senesced with decreasing autumn day length. Higher frequency reductions in daily GPP were associated with days with high precipitation and/or low PAR (Figure 7.1).

Daily GPP estimates ranged from 0.13 to 15.29 g CO₂-C m⁻² d⁻¹ in 2009 and from 0.07 to 15.84 g CO₂-C m⁻² d⁻¹ during 2010. Average (daily) GPP (Table 7.1) was higher during all months of 2009 than 2010, excluding July when the maximum daily values were observed for both years (and March with only partial data coverage), and at all other timeframes considered (i.e. summer, May to October and for the total measurement period).

Daily GPP increased steadily at WSF during warm conditions in spring 2009. In contrast, the delayed start of the 2010 growing season resulted in lower daily GPP during spring and early summer (Figure 7.1). GPP was considerably lower during early May in 2010 than for the corresponding period of 2009, although photosynthesis increased rapidly as conditions warmed towards the middle of the month (Figure 7.1). Maximum rates of daily GPP occurred in June in 2009 (mean of 11.84 g CO₂-C m⁻² d⁻¹), although average daily GPP was of similar magnitude in July (mean of 11.45 g CO₂-C m⁻² d⁻¹. Maximum rates of daily GPP (mean of 12.59 g CO₂-C m⁻² d⁻¹ for the study period were observed during warm conditions in July 2010 (Table 7.1) and were associated with the significant increase in vegetation activity as indicated by EVI (Figures 5.6 & 7.1).

Daily assimilation declined progressively following the seasonal peak during late summer and autumn in 2009 (Figure 7.1). In contrast, the onset of wet conditions with strongly reduced levels of irradiance in August 2010 resulted in lower daily assimilation rates relative to the same month of 2009, with monthly average assimilation rates of 8.52 ± 0.08 and 7.73 ± 0.09 g CO₂-C m⁻² d⁻¹, respectively. Daily GPP showed a brief increase during a period of more favourable conditions in late summer 2010 (Figure 7.1), before declining more rapidly throughout the cooler autumn conditions compared to the respective period of 2009 (Figure 7.1 & Table 7.1). Higher daily GPP during warm and dry conditions in autumn 2009 suggest ecosystem production was relatively insensitive to dry late season conditions at this fen. Minimum rates of daily photosynthesis were estimated for December in both years (Figure 7.1 & Table 7.1).

	GPP g CO ₂ -C m ⁻² d ⁻¹		ER g CO ₂ -C $m^{-2} d^{-1}$		$\frac{\mathbf{NEE}}{\mathrm{g}\mathrm{CO}_2\text{-}\mathrm{C}\mathrm{m}^{-2}\mathrm{d}^{-1}}$	
	2009	2010	2009	2010	2009	2010
March*	1.12 (0.02)	1.26 (0.02)	1.44 (0.01)	1.72 (0.01)	0.32 (0.02)	0.46 (0.02)
April	2.9 (0.08)	2.33 (0.04)	2.32 (0.03)	1.84 (0.02)	-0.58 (0.06)	-0.49 (0.03)
May	7.35 (0.13)	5.12 (0.1)	4.69 (0.05)	3.18 (0.06)	-2.66 (0.09)	-1.93 (0.05)
June	11.84 (0.13)	10.6 (0.17)	7.63 (0.07)	7.41 (0.12)	-4.21 (0.11)	-3.19 (0.12)
July	11.45 (0.12)	12.59 (0.12)	9.98 (0.03)	10.9 (0.04)	-1.46 (0.11)	-1.68 (0.12)
August	8.52 (0.08)	7.73 (0.09)	9.27 (0.04)	8.81 (0.07)	0.75 (0.09)	1.08 (0.08)
September	5.11 (0.06)	4.96 (0.11)	7.97 (0.06)	6.17 (0.03)	2.86 (0.07)	1.21 (0.1)
October	2.71 (0.07)	2.41 (0.05)	6.27 (0.04)	4.29 (0.07)	3.56 (0.07)	1.87 (0.05)
November	1.05 (0.03)	0.91 (0.02)	4.01 (0.03)	2.2 (0.04)	2.96 (0.04)	1.29 (0.04)
December	0.44 (0.01)	0.36 (0.01)	1.89 (0.03)	1.26 (0.01)	1.46 (0.03)	0.91 (0.01)
Summer (JJA)	10.59 (0.25)	10.30 (0.30)	8.98 (0.14)	9.06 (0.21)	-1.61 (0.28)	-1.25 (0.26)
May to October	7.82 (0.27)	7.23 (0.29)	7.64 (0.05)	6.79 (0.21)	-0.19 (0.24)	-0.44 (0.18)
20th March to 31st December	5.72 (0.25)	5.06 (0.26)	6.01 (0.17)	4.99 (0.20)	0.30 (0.17)	-0.08 (0.12)

Table 7.1: Monthly and seasonal averages of total daily gross primary production, ecosystem respiration and net ecosystem CO_2 exchange estimated for Wicken Sedge Fen using 2009 and 2010 data.

Daily ER showed a similar overall seasonal pattern to GPP at WSF (Figure 7.1). Estimates of daily ER ranged from 1.17 to 10.85 g CO₂-C m⁻² d⁻¹ in 2009 and from 0.94 to 11.84 g CO₂-C m⁻² d⁻¹ in 2010 at WSF. Similar to GPP, daily ER showed a steady increase throughout spring 2009. Daily ER remained low during cool spring conditions in 2010 (with generally higher water levels), but increased rapidly as conditions warmed in late May (Figure 7.1). Maximum rates of daily ER were estimated for July in both years, with monthly averages of 9.98±0.03 and 10.9±0.04 g CO₂-C m⁻² d⁻¹ in 2009 and 2010, respectively. Higher rates of daily ER in July 2010 were associated with the warmer and drier conditions and lower water levels that characterised this period (Figure 7.1).

In 2009, declining late season water levels and generally warmer conditions resulted in high rates of ER during late summer and autumn (Figure 7.1 and Table 7.1). By contrast, daily ER showed a strong reduction following the rapid rise in water levels during late August 2010 (Figure 7.1). ER remained significantly lower than during the previous year throughout the period of seasonal decline (Table 7.1). Although this pattern is partly explained by higher autotrophic respiration rates, and warmer temperatures, these differences clearly reflect the influence of water levels on late-season respiration rates at this peatland.

Seasonal differences in assimilatory and respiratory activity led to considerable between-year differences in NEE at WSF. Daily NEE ranged from -7.45 to 5.65 g CO₂-C m⁻² d⁻¹ and -6.81 to 5.09 g CO₂-C m⁻² d⁻¹ in 2009 and 2010, correspondingly. The onset of sink activity at WSF (defined as the first of five days with negative NEE) occurred on 17th and 8th April in 2009 and 2010, respectively (9 days earlier in 2010). NEE became more negative over the spring and early summer in both years, although positive values were observed when GPP was reduced during days with low irradiance/high rainfall. Net CO₂ uptake was generally higher during spring and early summer in 2009, whereas average daily NEE was greater during July of 2010 (Table 7.1). Minimum daily NEE values (i.e. highest net daily uptake) were observed on 14th and 4th June in 2009 and 2010, respectively.

In both years, daily NEE became gradually more positive as ER began to outpace GPP from midsummer onwards (Figure 7.1). WSF alternated between a daily net sink and a daily net source for CO_2 on wet and dry days, respectively, during late July and early

August in 2009. Declining late season water levels and subsequently high rates of ER resulted in the site becoming a net source for atmospheric CO₂ from 23^{rd} August onwards in 2009, representing a net sink period of 129 days (117 days with negative NEE). The highest net daily CO₂ effluxes occurred during late October in 2009 (monthly average of 3.56 g CO₂-C m⁻² d⁻¹), corresponding to the period of low autumn water levels and declining photosynthesis.

In 2010, the fen was generally (with only a few exceptions) a daily net source for CO_2 during wet conditions in August. The highest observed net daily CO_2 efflux was observed on 26th August in 2009, corresponding to a significant reduction in daily GPP on the wettest day of the year (experiencing 37 mm rainfall). A short period of net CO_2 uptake occurred as conditions improved in September, before the fen switched to a net daily source of CO_2 from 10th September 2010 onwards (19 days later than the previous year), and resulting in a (potential) sink period of 156 days (120 days with negative NEE). Net daily CO_2 losses remained considerably lower than in 2009 for the remainder of 2010 (Table 7.1).

7.2.2 Comparison of Bakers Fen and Wicken Sedge Fen in 2010

Figure 7.2 shows seasonal change in daily CO_2 budgets and environmental variables for BF during 2010. The WSF data for the period of paired measurements are shown for comparison (WSF data are reproduced from Figure 7.1). Daily GPP and ER at BF showed a broadly similar seasonal pattern to WSF during 2010 (during the period of paired measurements). However, daily assimilation and ER appeared more responsive

to higher frequency variations in meteorological conditions at the regenerating fen, illustrated by more pronounced peaks (depressions) in daily assimilation and respiration sums during periods of higher (lower) irradiation and warmer (cooler) conditions (Figure 7.2).



Figure 7.2: Seasonal change in daily carbon dioxide budgets and environmental variables at Wicken Sedge Fen (top panel) and Bakers Fen (second top) in 2010. Green and red bars show daily sums of gross primary production and ecosystem respiration; black bars are total daily net ecosystem exchange. PAR is total daily PAR (measured at BF); T_{air} is daily average air temperature; EVI is enhanced vegetation index; water level is the mean daily position of water levels relative to the fen surface. Bakers Fen water level data are shown for Diver 1. P is daily precipitation measured at BF.

Daily GPP ranged from 0.02 to 17.95 g CO₂-C m⁻² d⁻¹ at BF in 2010. Daily photosynthesis was low at the start of 2010 (Table 7.2), with the lowest daily values

observed in January and December (both with a mean of 0.27 ± 0.01 g CO₂-C m⁻² d⁻¹). Photosynthesis was not completely dormant at BF during the winter months and started to increase as soon as thermal conditions became suitable for plant growth in mid-March. Daily assimilation increased more rapidly at BF than at WSF during the spring months (Table 7.2), consistent with the earlier greening of the regenerating site (Figure 5.6 and Figure 7.2) and the earlier increase in the photosynthetic (α and GPP₁₅₀₀) parameters (Chapter 6).

A significant increase in daily GPP occurred at BF with the onset of warm conditions in late June, when daily assimilation showed a marked increase of ~5 g CO₂-C m⁻² d⁻¹ m⁻² d⁻¹. This increase was associated with a period of rapid phenological change at BF, when the dominant grass species entered their reproductive phase. Such a change was not evident at WSF, when the dominant plants complete their reproductive cycle towards the end of the growing season. The highest average daily assimilation rates (monthly average of 12.04±0.17 g CO₂-C m⁻² d⁻¹) occurred in June at BF (Table 7.2), although daily GPP was variable during this month (Figure 7.3), reflecting the period of rapid vegetation change.

GPP declined rapidly following the seasonal peak at BF. This most likely reflects reduced assimilation rates during the post-reproductive period of the dominant grasses, as well as increasingly dry soil conditions from late June onwards. Daily assimilation rates were lower than at WSF during July and August (Table 7.2). GPP declined less rapidly at BF than at WSF during autumn. Daily photosynthesis was higher at the regenerating fen between September and November (Table 7.2). Average daily GPP

was of similar magnitude at both sites during December (Table 7.2). On a seasonal basis, mean daily assimilation rates were lower at BF than at WSF during the summer months (June through August), but higher at BF than at WSF when the growing season (May to October) and period of paired measurements were considered (Table 7.2).

Table 7.2: Comparison of monthly, seasonal and annual averages (and standard error) of total daily gross primary production, ecosystem respiration and net ecosystem CO_2 exchange estimated for Wicken Sedge Fen and Bakers Fen in 2010. Note that data for March (marked with a *) for WSF are for the period 20th to 31st March only. WSF data are the same as in Table 6.1 and reproduced to enable direct comparison.

	GPP g CO ₂ -C m ⁻² d ⁻¹		\mathbf{ER} g CO ₂ -C m ⁻² d ⁻¹		\mathbf{NEE} g CO ₂ -C m ⁻² d ⁻¹	
-	WSF	BF	WSF	BF	WSF	BF
January		0.27 (0.01)		0.81 (0.01)		0.53 (0.01)
February		0.40 (0.01)		0.80 (0.01)		0.40 (0.01)
March*	1.26 (0.02)	0.99 (0.03)	1.72 (0.01)	1.19 (0.03)	0.46 (0.02)	0.20 (0.01)
April	2.33 (0.04)	4.42 (0.09)	1.84 (0.02)	2.96 (0.06)	-0.49 (0.03)	-1.46 (0.05)
May	5.12 (0.1)	7.70 (0.11)	3.18 (0.06)	5.33 (0.10)	-1.93 (0.05)	-2.38 (0.06)
June	10.6 (0.17)	12.04 (0.17)	7.41 (0.12)	9.39 (0.16)	-3.19 (0.12)	-2.65 (0.08)
July	12.59 (0.12)	10.68 (0.13)	10.9 (0.04)	10.31 (0.08)	-1.68 (0.12)	-0.37 (0.08)
August	7.73 (0.09)	6.73 (0.06)	8.81 (0.07)	7.86 (0.07)	1.08 (0.08)	1.12 (0.08)
September	4.96 (0.11)	5.60 (0.08)	6.17 (0.03)	7.04 (0.06)	1.21 (0.1)	1.43 (0.08)
October	2.41 (0.05)	3.17 (0.05)	4.29 (0.07)	4.67 (0.06)	1.87 (0.05)	1.50 (0.05)
November	0.91 (0.02)	1.25 (0.03)	2.2 (0.04)	2.70 (0.06)	1.29 (0.04)	1.45 (0.04)
December	0.36 (0.01)	0.27 (0.01)	1.26 (0.01)	1.17 (0.01)	0.91 (0.01)	0.91 (0.01)
Summer (JJA)	10.30 (0.30)	9.79 (0.34)	9.06 (0.21)	9.18 (0.24)	-1.25 (0.26)	-0.61 (0.22)
May to October	7.23 (0.29)	7.64 (0.27)	6.79 (0.21)	7.42 (0.20)	-0.44 (0.18)	-0.22 (0.16)
20th March to 31st December	5.06 (0.26)	5.59 (0.25)	4.99 (0.20)	5.55 (0.20)	-0.08 (0.12)	-0.04 (0.12)
Annual		4.48 (0.22)		4.54 (0.19)		0.06 (0.09)

ER showed a similar overall seasonal pattern to GPP at the regenerating fen (Figure 7.2). Estimates of accumulated daily ER ranged from 0.55 to 14.43 g CO₂-C m⁻² d⁻¹ at BF in 2010. Daily ER was low at the start of 2010, with the lowest daily values estimated for January and February (Table 7.2). ER increased steadily as conditions

warmed and the vegetation developed during spring and early summer. The most rapid increase in daily ER was associated with the period of rapid vegetation change in June (Figure 7.2), indicative of a strong contribution from autotrophic respiration. Daily ER declined rapidly following the seasonal maximum. Daily respiration rates were lower at BF than at WSF during July and August (Table 7.2), most likely explained by the combination of lower water levels (i.e. higher heterotrophic respiration) and vigorous plant activity (i.e. higher autotrophic respiration) at WSF during the midsummer period.

The seasonal pattern of NEE was similar at BF and WSF during the period of paired measurements (Figure 7.2). Daily estimates of NEE ranged from a net loss of 4.92 g $CO_2-C m^{-2} d^{-1}$ to a net gain of -4.85 g $CO_2-C m^{-2} d^{-1}$. BF was functioning as a small net source for CO_2 on a daily basis at the start of 2010, with the lowest daily CO_2 effluxes (mean of 0.21±0.01 g $CO_2-C m^{-2} d^{-1}$) observed during March (Table 7.2). Daily NEE became gradually more negative as spring progressed, the onset of the sink period occurring on 1st April (seven days earlier than at WSF). Similar to WSF, days with low irradiance during the growing season were associated with less negative NEE or net daily CO_2 efflux (Figure 7.2). Net uptake increased during spring and early summer, with daily NEE becoming most negative in June. Average daily NEE was more negative at BF than WSF in April and May, but less negative during June and July (Table 7.2).

Similar to WSF, daily NEE became gradually more positive from midsummer onwards at BF as GPP declined more rapidly than ER during the late summer (Figure 7.2). The regenerating fen was generally a net daily source throughout August (with only a few days of net uptake). A short period of net daily uptake was also observed at BF during more favourable conditions in early autumn (Figure 7.2), at a time when soil moisture content had increased after heavy rainfall in August (Figure 5.5).

BF switched to a net daily source for atmospheric CO_2 on 6th September 2010 (seven days earlier than at WSF), resulting in a total (potential) net sink period of 159 days in 2010 (126 days with net CO_2 uptake). With the exception of October, average net daily CO_2 effluxes were slightly higher at BF than at WSF between August and December 2010 (Table 7.2), consistent with greater photosynthetic activity (i.e. larger contributions from autotrophic respiration) during autumn, as well as lower late season water levels at the regenerating fen (Figure 7.2) in the absence of autumn water abstractions.

7.3 Monthly, seasonal and annual CO₂ budgets

Figure 7.3 (left) compares monthly totals of GPP, ER and NEE at WSF and BF during 2009 and 2010 (data for the partial month of March at WSF have been omitted). Data are the same as shown in Figures 7.1 and 7.2, but reproduced at the monthly timescale for more effective comparison with monthly meteorological data (Chapter 5). The left panels of Figure 7.3 present a comparison of monthly CO₂ exchange for WSF in 2009 and 2010; the right panels compare monthly CO₂ values of WSF and BF in 2010. 2010 data for WSF are the same in the left and right panels (shown in green in both).



Figure 7.3: Comparison of monthly gross primary productivity, ecosystem respiration and net ecosystem CO_2 exchange at Wicken Sedge Fen and Bakers Fen. Monthly meteorological variables are also provided. Data are the same as in Figures 7.1 and 7.2. Data shown in green are the same in the left and right subplots and are reproduced to aid comparison.

7.3.1 Wicken Sedge Fen

Total monthly GPP and ER were higher during all months of 2009 relative to 2010 at WSF with the exception of July 2010 when the highest monthly GPP and ER were observed for the study period (Figure 7.3 and Table 7.3). This pattern is broadly consistent with the observed pattern of monthly air temperature in 2009 and 2010, highlighting the importance of the thermal regime on both flux terms (GPP and ER) at this fen.

The largest between-year difference in total monthly GPP (82.52 g CO₂-C m⁻² month⁻¹) was observed during May, corresponding to the spring month with the largest temperature difference (Figure 7.3). In 2009, the highest total monthly assimilation occurred during June at 356.03 g CO₂-C m⁻² month⁻¹, but with similar a value of 355.71 g CO₂-C m⁻² month⁻¹ in July. Total monthly ER peaked at 310.33 g CO₂-C m⁻² month⁻¹ during warm and dry conditions in July in 2009 (Table 7.3). Total monthly GPP and ER both peaked during July in 2010 at 391.70 and 339.48 g CO₂-C m⁻² month⁻¹, correspondingly. In 2009, total monthly ER was significantly higher than in 2010 between September and December. The largest between-year difference in accumulated monthly ER was observed for October at WSF with a value of 61.23 g CO₂-C m⁻² month⁻¹. This difference was associated with a significant between-year difference in water levels, as well as higher monthly average temperature (Figure 7.3).

Net CO₂ uptake occurred between April and July in both years at WSF (Figure 7.3). The highest net monthly uptake of -126.40 g CO₂-C m⁻² month⁻¹ was observed during June 2009. This reflects the earlier peak in (monthly) GPP in 2009 compared to 2010, occurring at a time when ER had yet to attain a seasonal maximum. Net CO₂ uptake was greater during all months of spring and early summer of 2009 than during 2010, but was marginally higher during July 2010 than in 2009 (Figure 7.3). The highest observed monthly ER during this month was compensated by an even stronger increase in monthly GPP during warmer and drier than average conditions. This finding contrasts with results from other peatlands, where warm and dry summer conditions are often associated with a reduction in net CO₂ uptake (e.g. Alm *et al.*, 1999; Bubier *et al.*, 2003; Aurella *et al.*, 2007; 2009; Cai *et al.*, 2010; Sonnentag *et al.* 2010).

WSF functioned as a net CO_2 source between August and December in 2009 and 2010. The highest net monthly CO_2 efflux occurred in October of both years at 110.37 and 58.05 g CO_2 -C m⁻² month⁻¹, respectively (Table 7.3), a net difference of 52.32 g CO_2 -C m⁻² month⁻¹. In 2009, net CO_2 losses between September and December were significantly higher than for the corresponding months of 2010. This was due to higher monthly ER in 2009 when water levels were significantly lower relative to 2010 (Figure 7.3 and Table 7.3). In September and November 2009, the total net CO_2 efflux was more than double the magnitude of monthly CO_2 loss during the same months of 2010 (Table 7.3). These large (reduced) late-season CO_2 fluxes clearly reflect the influence of low (high) late season water levels on C mineralisation rates at this peatland during 2009 (2010). Significantly lower net losses in December 2010 compared to the previous year reflected the unusually cold conditions of this month, as water levels had reached similar levels by this time (Table 7.3).

For the complete measurement periods (20th March to 31st December), the semi-natural fen functioned as a net source of 85.47 ± 25.78 g CO₂-C m⁻² period⁻¹ in 2009 and a small net sink of -22.66±18.85 g CO₂-C m⁻² period⁻¹ in 2010 (Table 7.3 and Figure 7.4). *u** selection was the largest source of uncertainty in the time integrated estimates of NEE at this WSF. The uncertainty range for 2010 indicates WSF may have been close to the CO₂ compensation point in 2010. The total between-year difference in NEE was estimated at *circa* 108 g CO₂-C m⁻² period⁻¹.

Estimates of total accumulated GPP and ER were both higher during the generally warmer conditions of 2009 than 2010 (Figure 7.4). This is consistent with the higher

radiation in 2009, and the longer thermal season compared to 2010. Accumulated GPP was estimated at 1589.96 and 1458.82 g CO₂-C m⁻² period⁻¹ in 2009 and 2010, respectively, a net difference of approximately 131 g CO₂-C m⁻² period⁻¹ (Figure 7.4). Cumulative ER was estimated at 1675.44 g CO₂-C m⁻² period⁻¹ in 2009, and 1436.18 g CO₂-C m⁻² period⁻¹ in 2010 (Figure 7.4), corresponding to a net difference of around 239 g CO₂-C m⁻² period⁻¹.



Figure 7.4: Accumulated gross primary production (top left), ecosystem respiration (lower left) and net ecosystem exchange (top right) at Wicken Sedge Fen for 2009 and 2010. Data are for the period 20th March to 31st December.

Table 7.3: Monthly, seasonal and annual sums of gross primary productivity, ecosystem respiration and net ecosystem exchange measured at Wicken Sedge Fen and Bakers Fen during 2009 and 2010. Note that data for March 2009 and 2010 are for the period 20^{th} to 31^{st} March in both years. Uncertainty estimates are provided for seasonal and annual sums of NEE only. All units are in g C m⁻².

Time period	Wick	Wicken Sedge Fen 2009Wicken Sedge Fen 2010			Bakers Fen 2010				
	GPP	ER	NEE	GPP	ER	NEE	GPP	ER	NEE
		g CO ₂ -C n	m ⁻²		g CO ₂ -C 1	m ⁻²		g CO ₂ -C	m ⁻²
January							8.43	24.97	16.55
February							11.18	22.38	11.20
March*	13.42*	17.29*	3.87*	15.15*	20.70*	5.55*	30.73	36.83	6.10
April	87.25	69.75	-17.50	70.05	55.44	-14.61	132.68	88.94	-43.74
May	228.60	146.08	-82.52	158.85	98.96	-59.89	238.81	165.09	-73.71
June	356.03	229.63	-126.40	318.64	222.89	-95.76	361.12	281.76	-79.36
July	355.71	310.33	-45.38	391.70	339.48	-52.23	331.13	319.53	-11.59
August	264.66	287.94	23.28	240.58	273.50	32.92	208.78	243.57	34.79
September	154.04	239.91	85.87	149.30	185.68	36.38	168.12	211.06	42.94
October	84.64	195.02	110.37	75.73	133.79	58.05	98.26	144.70	46.43
November	31.82	120.52	88.70	27.55	66.35	38.80	37.53	80.98	43.45
December	13.79	58.97	45.18	11.27	39.39	28.12	8.23	36.42	28.19
June July, August	976.40	827.90	-148.50	950.92	835.87	-115.07	901.03	844.86	-56.17
May to October	1443.68	1408.91	-34.7	1334.80	1254.30	-80.53	1406.22	1365.71	-40.51
20th March to 31st December	1589.96	1675.44	85.47±25.78	1458.82	1436.18	-22.67±18.85	1603.68	1593.45	-10.23±14.68
Annual							1634.99	1656.24	21.24±17.11

Notes: Values marked with a * are only partial monthly estimates.
Site / time period	20%	Spike removal	u^*	Gap-filling	Gap-filling R_g	Total
Site / time period	g C m ⁻² period ⁻¹	Totai				
WSE 2000 (20 th Moreh to 21 st	17.00	256	10 70	2.65	0.02	25 78
December 2009)	17.09	2.30	18.78	5.05	0.05	23.78
WSF 2010 (20 th March to 31 st December 2010)	4.44	4.43	17.56	2.82		18.85
BF 2010 (all)	4.25	6.50	10.78	10.78		17.11
BF 2010 (20 th March to 31 st December 2010)	2.04	3.45	10.44	9.51		14.68

Table 7.4: Summary of uncertainties estimated for seasonal and annual estimates of net ecosystem CO₂ exchange at Wicken Sedge Fen and Bakers Fen.

Notes: The column marked: 20% refers to the \pm 20% measurement error applied to seasonal and annual estimates of NEE; spike removal is the standard deviation of summed estimates of gap-filled NEE generated using *z*-values of 4.5, 5 and 7 in the outlier detection routine (after Papale *et al.*, 2006); *u** is the standard deviation of NEE sums generated using *u** filters of 0.05, 0.1 and 0.15 m s⁻¹; gap-filling is the uncertainty introduced by data gap-filling as estimated by the online algorithm of Reichstein *et al.* (2005a); gap-filling of R_g refers to uncertainty introduced by the gap-filling or R_g and is only applicable to 2009. Total uncertainty was calculated using the error accumulation principle (equation 7.1).

7.3.2 Bakers Fen

The BF site was a small net source of 21.24 ± 17.11 g CO₂-C m⁻² yr⁻¹ for the complete annual cycle of 2010 (Figure 7.5 and Table 7.3). *u** filtering and data gap-filling introduced were the largest sources of uncertainty in terms of the annual estimate of NEE (Table 7.4). The results of the flux partitioning indicate cumulative annual GPP was 1634.99 g CO₂-C m⁻² yr⁻¹ with accumulated losses via ER totalling 1656.24 g CO₂-C m⁻² yr⁻¹ (Figure 7.5 and Table 7.3).

Total monthly assimilation was highest in June at 361.12 g CO₂-C m⁻² month⁻¹, whereas accumulated monthly ER peaked at 319.53 g CO₂-C m⁻² month⁻¹ during warm conditions in July. The lowest monthly GPP and ER were both observed in December and January, at 8.23 and 24.97 g CO₂-C m⁻² month⁻¹, correspondingly (Figure 7.5 and Table 7.3). The regenerating fen functioned as a net sink for atmospheric CO₂ between April and July and a net source during all other months (Figure 7.3). The highest net monthly uptake of -79.36 g CO₂-C m⁻² month⁻¹ occurred during June; the highest net monthly CO₂ efflux of 46.43 g CO₂-C m⁻² month⁻¹ was observed in October (Table 7.3).

Total NEE during the thermal growing season (13th March to 23rd November in 2010) was -42.15 g CO₂-C m⁻² period⁻¹. Total CO₂ losses outside of this period were estimated at 63.39 g CO₂-C m⁻² period⁻¹. The non-growing season CO₂ loss at BF was equivalent to ~300% of the absolute magnitude of the annual CO₂ exchange. Similar to other studies (e.g. Aurella *et al.*, 2002) this highlights the importance of capturing the low but persistent net CO₂ efflux outside of the main growing season.



Figure 7.5 Accumulated gross primary productivity (top left), ecosystem respiration (lower left) and net ecosystem exchange (right) measured at Bakers Fen during 2010.

7.3.3 Wicken Sedge Fen and Bakers Fen in 2010

Monthly GPP and ER were higher at BF than WSF for all months of the paired measurement period, excluding July and August (Figure 7.3 and Table 7.3). The largest between-site differences in total monthly GPP and ER occurred during May, at 79.96 and 66.13 g CO₂-C m⁻² month⁻¹, correspondingly, and were both higher at BF (Figure 7.4 and Table 7.3). A considerable difference in total monthly photosynthesis was also observed in July (Figure 7.4 and Table 7.3), when monthly GPP at WSF exceeded that of BF by 60.57 g CO₂-C m⁻² month⁻¹.

Total net CO_2 uptake was higher at the regenerating fen during April and May but lower than at WSF in June and July (Figure 7.3 and Table 7.3). The largest absolute difference in monthly NEE occurred during July with the highest uptake at WSF (Table 7.3) at 40.64 g CO₂-C m⁻² month⁻¹. Monthly net CO₂ losses were generally higher at BF than at WSF from August onwards, with the exception of October (Figure 7.3). Despite differences in GPP and ER, the total net CO₂ efflux estimated for the latter interval was of similar magnitude at 194.27 and 195.8 g CO₂-C m⁻² period⁻¹ at BF and WSF, respectively (Table 7.3).

Figure 7.6 compares accumulated GPP, ER and NEE for the paired measurement period at WSF and BF in 2010. It should be noted that Figure 7.6 (and the following values in the text) represent the paired period during which both towers were operating under near-identical weather conditions. Lower accumulated values for BF (relative to the annual estimate presented above and Figure 7.5) are due to the omission of flux data for the period 1st January to 19th March 2010, when the assimilatory flux was low, and losses via ER relatively high with respect to GPP.



Figure 7.6: Comparison of cumulative gross primary production, ecosystem respiration and net ecosystem exchange estimated for Wicken Sedge Fen and Bakers Fen in 2009 and 2010. Data are for the period 20^{th} March to 31^{st} December 2010. Note that the data for BF are the same as those presented in Figure 7.5. The Bakers Fen site was a net sink during the paired measurement period as net CO₂ losses over the period 1^{st} January to 19^{th} March have been omitted.

Accumulated NEE at BF for the period 20th March to 31st December was estimated at - 10.23 ± 14.68 g CO₂-C m⁻² period⁻¹. As noted above, the BF site was a small annual source for atmospheric CO₂ in 2010. The small net sink for the paired measurement period reflects the omission of flux data for the late winter and early spring period when the site was losing C in the form of CO₂. Of the NEE for the paired measurement period, 1603.68 and 1593.45 g CO₂-C m⁻² period⁻¹ were attributed to GPP and ER, respectively (Table 7.3). Accumulated GPP and ER were both higher at BF than at

WSF over the paired measurement interval (Figure 7.6), with net differences of 144.86 and 157.27 g CO₂-C m⁻² period⁻¹, correspondingly (Table 7.3).

The between-site difference in time-integrated NEE for the paired measurement period was small at 12.44 g CO₂-C m⁻² despite considerable seasonal differences in the pattern of CO₂ exchange the two sites. WSF was the larger sink for atmospheric CO₂ during this period (top right in Figure 7.6). Total CO₂ loss at BF for the period 1st January to 19th March (the period of missing data at WSF) was estimated at 32.23 g CO₂-C m⁻² period⁻¹, equivalent to ~150% of the absolute magnitude of the annual NEE estimated for BF during 2010. If similar CO₂ losses are assumed for WSF for the start of the year, it is likely that the semi-natural fen was either close to CO₂ neutral or a small net CO₂ source in 2010, and a larger net source in 2009. Although such similarity cannot simply be assumed, this further highlights the need to capture winter and early spring CO₂ fluxes at the semi-natural fen.

7.4 Chapter Summary

This chapter has presented and compared daily, monthly and seasonal estimates of accumulated NEE and its component fluxes at WSF and BF. An annual CO_2 budget was presented for the regenerating former arable fen. Similar overall seasonal patterns in NEE and its component fluxes were observed for both years at WSF and at both sites in 2010. Despite this overall similarity, marked differences were observed in the seasonal magnitude of accumulated CO_2 exchange.

The contrasting environmental conditions of 2009 and 2010 had a strong influence on the seasonal magnitude of CO_2 exchange at WSF. In general, warmer and drier conditions were associated with higher rates of accumulated GPP and ER at this peatland (i.e. indicated by daily averages and monthly sums). WSF functioned as a net (monthly) sink between April and July in both years, although daily CO_2 budgets show the net uptake period was longer in 2010. Higher rates of photosynthesis in spring and early summer 2009 resulted in higher net CO_2 uptake compared to 2010. Net uptake was higher in July of 2010, as maximum observed rates of total ER were outweighed by even higher accumulated GPP. Warmer temperatures and low water levels resulted in high rates of ER and large net CO_2 losses during autumn 2009. In contrast, high water levels following extremely wet conditions in August significantly reduced ER and net CO_2 losses in autumn 2010.

Considerable differences in the seasonal magnitude of CO_2 exchange were observed at WSF and BF in 2010. GPP and ER (i.e. average daily values and monthly sums) were generally higher at the regenerating fen, except during June and July, when both flux terms were greater at WSF. Similar to WSF, BF functioned as a net sink between April and July, although the regenerating site had slightly more days with negative NEE. Net CO_2 uptake rates were higher during spring at BF, but greater at WSF during June and July. During the late summer and autumn, differences in GPP and ER were effectively balanced, resulting in similar late season CO_2 effluxes. A short period of net CO_2 uptake was observed during early September at both sites.

The semi-natural fen functioned as a net source of 85.47 ± 25.78 g CO₂-C m⁻² period⁻¹ between 20th March and 31st December 2009 and a small net sink of -22.66±18.85 g

 CO_2 -C m⁻² during the same period of 2010. GPP and ER were both enhanced during 2009 compared to 2010. The increase in ER outweighed the increase in GPP, mainly due to enhanced ER during the dry conditions of the late season. The regenerating fen was a small net source of 21.24±17.11 g CO₂-C m⁻² yr⁻¹ in 2010. Despite differences in the seasonal pattern of GPP and ER at the two fens, accumulated NEE for the paired measurement period of 2010 at BF was of similar magnitude to WSF at -10.23±14.68 g CO_2 -C m⁻² period⁻¹.

Chapter 8: Discussion and conclusions

This chapter provides a discussion of the results presented in the previous chapters and draws conclusions based on the findings of this thesis. The first part of the chapter discusses the results in light of the research questions posed by this study. The implications of the results are discussed in terms of peatland management under projected climate changes. The second part of the chapter identifies and discusses the limitations of the research presented. Potential avenues for improvement and/or future study are discussed. The chapter concludes with a synopsis of the main findings of this thesis.

8.1 Addressing the research questions

8.1.1 Factors influencing land/atmosphere CO₂ exchange

At both fens, ecosystem phenology, modulated by seasonal and higher frequency variations in irradiance, temperature and moisture conditions were all important controls on the seasonal pattern and magnitude of NEE (Chapter 6). In the following sections, the environmental controls on GPP and ER are discussed. The influences of these CO_2 exchange processes on the seasonal pattern and magnitude of NEE are discussed in subsequent sections.

8.1.2 Gross primary production

Differences in the dominant vegetation communities at the study sites resulted in strong differences in the sensitivity of GPP to environmental conditions (Chapter 6). The BF

community was able to utilise available light more effectively, whereas the WSF vegetation attained higher maximum assimilation rates once the plant canopy had fully developed (Figures 6.7, 6.9 & 6.12; Tables 6.1, 6.2 & 6.4). These differences in light use characteristics are most likely explained in terms of lower levels of self-shading under the more open vegetation structure at BF (Jacobs *et al.*, 2007), and the larger peak season biomass (and presumably LAI) at WSF (e.g. Humphreys *et al.*, Lund *et al.*, 2010), correspondingly.

Differences in the temperature response and sensitivity of the two fens clearly reflect the phenology of the respective plant communities (Figure 5.6). At BF, photosynthesis was not entirely dormant over the cold winter months, and the agricultural grasses rapidly developed leaf area and photosynthetic capacity as soon as thermal conditions became suitable for growth. By contrast, the dominant species at WSF develop new shoots and photosynthetic tissue during the spring months, and do not attain maximum photosynthetic capacity until leaf area fully develops under warmer conditions later in the season. Further, the photosynthetic activity of the WSF plant community showed a more rapid decline as conditions cooled during autumn (Figures 6.9, 7.2 & 7.3; Table 7.2).

Inclusion of water levels as a predictor variable increased the diagnostic power of the GPP model at both study sites (Figure 6.12; Table 6.4). Increasing photosynthesis rates up to WL_{opt} at both fens likely reflects a combination of direct physiological responses of the vascular plants to increasing aeration (and most likely peat temperature) in the rhizosphere (Sulman *et al.*, 2010), as well as increased nutrient (i.e. N) mineralisation

rates (Lamers *et al.* 2002). Given the current vegetation at the BF site, WL_{tol} and WL_{opt} are consistent with the drainage requirements of -0.4 to -0.5 m typically required to maintain productive grasslands (i.e. grazing pastures) on peat substrates (Höper *et al.*, 2008). The reduction in photosynthesis beyond WL_{opt} at BF most likely reflects a direct physiological response of the grasses to declining soil water availability.

At WSF, a decline in assimilation rates below WL_{opt} could reflect species-specific responses from the dominant plants. P. australis, for example, is a deep-rooted species (up to 2 m), and is able to tap water from deep in the peat profile even during extended dry periods (Bennett & Friday, 1997; Kelvin, 2011). By contrast, C. mariscus forms a dense and laterally spreading root system in the near-surface layer (Friday & Harvey, 1997). A (slight) decline in photosynthesis below WL_{opt} may therefore reflect a reduction in C. mariscus photosynthesis due to increasing water stress, and/or a decline in (base) nutrients supplied by minerotrophic waters (Tuittila et al., 2004; Riutta et al., 2007a). Such species-specific responses could also explain why VPD appeared to be a more important control on NEE (via stomatal regulation of GPP) during the dry conditions of summer 2010 (Figures 6.14 and Table 6.5). Despite this, the highest observed rates of photosynthesis occurred during dry conditions in July 2010, indicating that high light levels, warm temperatures and higher leaf production (indicated by EVI) outweighed the influences of dry site and atmospheric conditions. This is consistent with Lindroth et al. (2007) who identified temperature as the strongest driver of GPP in a study of boreal mires.

8.1.3 Ecosystem respiration

At both sites, ER (expressed by R and daily and monthly estimates of ER) showed a similar overall seasonal pattern to photosynthetic activity (Chapters 6 and 7). Strong correlations were identified between monthly photosynthetic parameters and monthly (average) respiration rates (Figure 6.5; Table 6.3). These results are in line with other studies (e.g. Humphreys *et al.*, 2006; Lindroth *et al.*, 2007; Cai *et al.*, 2010), which show a strong dependence of the respiratory CO_2 efflux on the developmental stage and photosynthetic activity of plant communities via the supply of recent photosynthates to support autotrophic respiration, as well as the heterotrophic consumption of litter, roots and the exudates of vascular plants.

In terms of abiotic controls, ER was regulated by temperature and hydrological variation at both fens (Figures 6.15 to 6.17; Tables 6.6 to 6.8). At WSF, a clear dependence of ER on both temperature and water levels is consistent with findings from other (i.e. most) peatland studies (e.g. Silova *et al.*, 1996; Chimner & Cooper, 2003b; Bubier *et al.*, 2003; Lloyd, 2006; Sulman *et al.*, 2009; 2010). Although ER represents the combined response of auto- and heterotrophic contributions, a Gaussian response to water level variation is consistent with a positive relationship between heterotrophic respiration rates and the volume of habitat available to aerobic consumers (Hatala *et al.*, 2012). Increasing CO_2 efflux rates up to WL_{opt} were also likely associated with enhanced root respiration, increased gas diffusion rates, and higher peat temperatures (Chimner & Cooper, 2003b; Sulman *et al.*, 2010; Hatala *et al.*, 2012). The decline in ER at the lowest observed water levels is most likely explained by reduction in microbial activity as surface moisture conditions became limiting (Haapala *et al.*, *et al.*, 2013).

2009). Despite this reduction, CO_2 efflux rates remained high at the lowest water levels observed during this study (Figures 6.15 & 6.16).

ER at the regenerating ex-arable fen appeared to be more strongly regulated by temperature than either water levels or (relative) soil moisture in 2010. A stronger dependence of ER on temperature has also been reported at other peatlands (Lafleur *et al.*, 2005; Nieveen *et al.*, 2005; Jacobs *et al.*, 2007). Lafleur *et al.* (2005) suggested a relatively weak response to water level variation at a temperate (Canadian) bog could be explained by different responses from auto- and heterotrophic contributions, and interactions between down profile gradients in peat quality and water levels/soil moisture. For these reasons, these and other authors (e.g. Lloyd, 2006; Jacobs *et al.*, 2007; Parmentier *et al.*, 2009) suggest that stronger responses from ER should be expected at wetter peatlands.

At BF, the observed increase in ER along the hydrological gradient is part-explained by increasing contributions from autotrophic respiration as plant activity increased (decreased) as water/soil moisture levels declined (recovered) during spring (autumn). Given the site history and current vegetation at BF, it is possible that most of the labile organic material (i.e. litter, roots) is present close to the fen surface (Chimner & Cooper, 2003b). The relatively weak response to water level variation (compared to T_{air}) is potentially explained by low CO₂ production from the degraded (i.e. recalcitrant) deeper peat (Glatzel *et al.*, 2004; Berglund & Berglund, 2008; Leifeld *et al.*, 2012). This would also explain why (relative) soil moisture appears to play a secondary role to temperature, if most microbial activity was taking place in the layer above the CS616

sensor depth (e.g. Reichstein *et al.* 2005b). If confirmed, this implies water levels would need to be maintained at high levels to significantly influence surface moisture conditions and soil respiration rates (e.g. Parmentier *et al.*, 2009).

8.1.4 Seasonal patterns and flux magnitudes

A large seasonal variation in NEE was observed at the study sites. NEE and its component fluxes at both fens showed broadly similar overall seasonal patterns. CO_2 flux magnitudes were low during the early season, attained highest values when irradiance and temperature reached seasonal maxima, and declined as the vegetation senesced throughout autumn. In both years and at both sites, net CO_2 uptake occurred between April and July (on a monthly basis), with net CO_2 losses during all other months. Despite this overall similarity, large between-year and between-site differences in CO_2 flux densities were observed (Figures 7.1 to 7.3; Tables 7.1 to 7.3).

The sites investigated in this study both had high photosynthetic and respiratory capacity, WSF having higher peak season flux magnitudes than the regenerating fen (Tables 6.1, 7.1 & 7.3). Maximum estimates of α , GPP₁₅₀₀, and accumulated (i.e. daily) GPP were towards the higher end of values reported for (northern) peatlands (e.g. Humphreys *et al.*, 2006; Lund *et al.*, 2010), but were of similar magnitude to managed grasslands on organic soils (e.g. Veenendaal *et al.*, 2007; Shurpali *et al.*, 2009). Similarly, both ecosystems had higher basal respiration (R₁₀) and peak season rates of ER compared to more northerly sites (Silova *et al.*, 1996; Glenn *et al.*, 2006). These differences are largely explained by: (i) the large living plant biomass of the study sites

relative to more northerly (non-treed) peatlands (Humphreys *et al.*, 2006); (ii) higher heterotrophic respiration rates as a function of warmer temperatures and a large seasonal variation in water levels; and (iii) the extreme-rich (pH) status of the study sites (Lund *et al.*, 2010). Points (i) and (ii) also explain higher peak season flux densities at WSF compared to the regenerating BF site.

The contrasting meteorological conditions of 2009 and 2010 had a marked influence on the seasonal pattern of NEE at WSF. In general, warmer and drier conditions appeared to enhance both GPP and ER at this peatland (Figures 7.1 and 7.3). GPP largely controlled the direction and magnitude of NEE during the spring and summer months, whereas ER more strongly regulated the magnitude of CO_2 losses from midsummer onwards (Figures 6.4, 7.1 & 7.3). An exception to this was August 2010, where (marginally) higher net CO_2 losses were associated with a significant reduction in GPP under conditions of low irradiance, despite lower rates of (monthly) ER.

Warmer than average temperatures and the earlier development of the vegetation were associated with considerably higher assimilation and net CO_2 uptake rates during spring 2009 (Figures 7.1 & 7.2; Tables 7.1 & 7.3). By contrast, anomalously cool weather during spring 2010 (particularly during May) significantly reduced the metabolic activity of plants and soil microbial populations. The reduction in photosynthetic activity and net CO_2 uptake in 2010 clearly reflected the sensitivity of the phenological development of the dominant plant species to low temperatures (e.g. Zhou, Zhou & Jia, 2009, and late spring frosts in particular (Bennett & Friday, 1997; Friday & Harvey, 1997). A large reduction in spring uptake was also reported for a (restored) wetland in western Norway (Herbst *et al.*, 2012) during the anomalously cool conditions that affected northwest Europe in late winter and spring of 2010.

The influence of spring temperatures on ecosystem phenology continued into the early summer at WSF. In 2009, the earlier development of the vegetation during the warmer spring months resulted in an earlier and more negative peak in (monthly) net CO_2 uptake rates compared to 2010 (Figure 7.3). By contrast, the onset of warmer than average conditions during late June 2010 was associated with a considerable increase in photosynthetic and respiratory activity, and the highest observed CO_2 flux magnitudes. In contrast to results from other peatlands (e.g. Bubier *et al.*, 2003; Aurela *et al.*, 2007; 2009; Sonnentag *et al.*, 2010), photosynthesis was more strongly enhanced than ER during this warm and dry midsummer period, serving to enhance net CO_2 adsorption rates relative to same month of the preceding year.

The thermal and hydrological regimes had a strong influence on late-season CO_2 losses at WSF (and the time-integrated CO_2 balance – discussed below). In 2009, warmer and drier than average conditions resulted in higher rates of late-season GPP compared to 2010. This contrasts with results from other fens, where warm and dry conditions are often associated with reductions in assimilation rates and/or an early onset of plant senescence (e.g. Sonnentag *et al.*, 2010; Leppälä *et al.*, 2011). Most significant, however, was the influence of hydrological conditions on late-season CO_2 losses. The large variation in water levels effectively acted as a 'switch' to ER at WSF during the autumn months, with low (high) late-season water levels resulting in considerably higher (lower) releases of CO_2 during 2009 (2010), as well as a shorter (longer) net CO_2 uptake period in 2009 (2010).

The data from WSF and BF for the paired measurement period of 2010 are (currently) unique in illustrating the responses of a regenerating fen and an immediately adjacent semi-natural (reference) site to near-identical meteorological conditions. Despite considerable differences in plant community species composition (Stroh *et al.*, 2012), peat characteristics (i.e. peat quality and depth) (Morgan, 2005) and hydrological conditions (Figures 5.4, 5.5 & 7.2), the two sites showed comparable periods of net CO_2 uptake and net loss (i.e. 120 and 126 days with negative NEE at WSF and BF, correspondingly), and were very similar in terms of time-integrated (i.e. 20th March to 31st December 2010) estimates of NEE (discussed below).

The higher spring and early summer uptake at BF clearly reflects the earlier phenological development of the vegetation at the regenerating fen (Figures 5.6 & 7.2). As noted previously, the dominant species at BF developed photosynthetic tissue as soon as thermal conditions became suitable for plant growth. As such, the BF community was able to exploit high light conditions during the (cooler than average) spring months. By contrast, development of the photosynthetic capacity of the WSF community occurred later in spring, and resulted in significantly higher net CO_2 absorption rates over the summer period, despite much higher peak-season CO_2 efflux rates (Figure 6.3). It is also likely that the lower rates of net CO_2 uptake at BF during the summer months reflected a reduction in photosynthesis during the post-reproductive phase of the dominant grasses, and/or reduced levels of plant activity as a function of

water stress under increasingly dry site conditions from early summer onwards (Figure 5.5).

Net CO_2 losses were of similar magnitude at the two fens during the late summer and autumn in 2010 (Figure 7.2 & 7.3 Table 7.2). Higher (lower) rates of GPP and ER at BF (WSF) were approximately balanced in terms of the net CO_2 exchange. Higher rates of late-season photosynthesis at the regenerating fen are explained by the higher light use efficiency and broader temperature tolerance of the BF vegetation, and may also reflect the recovery (i.e. a late season flush) of the agricultural grasses following the increase in soil water levels during late summer. The higher rates of late-season ER at BF can largely be explained in terms of higher autotrophic respiration rates (Glenn *et al.*, 2006), but could also reflect a more rapid turnover of (the more labile) plant litter and drier site conditions compared to WSF (Figures 6.3 & 7.2). At both sites, the short period of net CO_2 uptake during September implies that the net CO_2 sink period (and overall sink strength) could be extended if hydrological conditions could be more effectively managed throughout the growing season (Figure 7.2).

8.1.5 Carbon dioxide budgets

The WSF site was a net source for atmospheric CO_2 between 20^{th} March and 31^{st} December in 2009 (85.47±25.78 g CO₂-C m⁻²) and a net sink during the corresponding period of 2010 (-22.67±18.85 g CO₂-C m⁻²). It was not possible to capture winter fluxes at WSF due to insufficient power requirements. Low but persistent net losses during the early part of the year would have made the site a larger net (annual) source in 2009 and

would likely have rendered the site close to CO_2 neutral if not a small net source in 2010 (e.g. Aurella *et al.*, 2002). The net loss of C in the form of CO_2 during the 2009 measurement period was equivalent to three to five times the magnitude of long-term C accumulation rates (15 to 30 g C m⁻² yr⁻¹) estimated for northern peatlands (Turanen *et al.*, 2002).

On a seasonal basis (i.e. 20^{th} March to 31^{st} December), accumulated GPP and ER were both enhanced at WSF during warmer and drier conditions of 2009. The between-year difference in accumulated GPP was mainly driven by differences in spring (and to a lesser degree autumn) photosynthesis. In 2010, the highest observed rates of GPP during warm and dry conditions in July proved relatively ineffective in compensating for spring reductions in terms of the cumulative GPP sum (Figure 7.4). This is consistent with earlier studies at (boreal) fens (Griffis *et al.*, 2000; Aurella *et al.*, 2004), which show seasonal and annual estimates of GPP are strongly influenced by environmental conditions during the period of spring green up.

The higher accumulated GPP at WSF in 2009 (relative to 2010) was outweighed by a larger increase in ER. In contrast to GPP, higher ER during warm and dry conditions (with low water levels) of summer 2010 part compensated for the reduction in ER during the cool spring (Figure 7.4). However, increased divergence in cumulative ER from late summer onwards had the strongest influence on the seasonal estimates of NEE (Figure 7.4). In 2009, higher late season ER effectively outweighed the benefits of higher net CO_2 absorption during the warm spring period, indicating that late season ER was the most important determinant of the between-year variation in NEE in 2009 and

2010. By contrast, the reduction in ER during late summer in 2010 was able to compensate for reduced rates of net uptake earlier in the year, rendering the site a net sink for atmospheric CO_2 over the period considered.

The partial annual estimate of NEE at WSF, and a general lack of data for temperate (European) fens with semi-natural vegetation cover (e.g. Couwenberg *et al.*, 2008), make comparisons with other sites challenging. However, a similar between-year variation in (seasonal) estimates of NEE has been reported for other northern peatlands. For example, a fen in northern Manitoba was a net sink of -92 g CO₂-C m⁻² between April and September in 1994, whereas the same peatland released 30 g CO₂-C m⁻² during the corresponding (warmer and drier) period of 1996 (Lafleur *et al.*, 1997; Joiner *et al.*, 1999). Similarly, Shurpali *et al.* (1995) reported an (ombrogenous) peatland in Minnesota had an NEE of 71 and -32 g CO₂-C m⁻² yr⁻¹ between May and October in 1991 (warm and dry) and 1992 (cooler and wetter), respectively. These studies and the results from WSF demonstrate the potential for large releases of C as CO₂ and potential feedbacks to climate change, should warmer and drier conditions become more frequent.

The CO_2 budgets for WSF in 2009 and 2010 illustrate the sensitivity of this peatland to climatic variability and change. Although two years represents a short measurement period, the large variation in NEE appear consistent with previous predictions of peatland responses to climate change, which suggest enhanced rates of GPP under warmer conditions and extended growing seasons will be outweighed by higher rates of CO_2 loss as a function of the direct (i.e. temperature) and indirect (i.e. lower water

levels) impacts of climate change (Gorham, 1991). In particular, it appears that the CO_2 balance of this site is sensitive to conditions during the shoulder seasons (spring and autumn). As such (other factors being unchanged), it is likely that the impacts of climate change on this ecosystem will depend (in part) on how projected climate changes (see Table 8.3 below) are manifest during the spring and autumn periods (e.g. Piao *et al.*, 2008).

The BF site functioned as a small net annual source for atmospheric CO_2 (22.67±18.85 g CO_2 -C m⁻² yr⁻¹) in 2010. This suggests the regenerating fen continued to lose small amounts of soil C after fifteen years under restoration management, at least over the annual period considered here. This relatively low annual CO_2 loss was somewhat surprising, given the inability to maintain high water levels (or surface soil moisture content) and the absence of a wetland (i.e. peat-forming) flora. It is possible that this low value may reflect a low CO_2 production potential from the recalcitrant peat layer (Glatzel *et al.*, 2004; Leifeld, Steffens & Galego-Sala, 2012), with most of the CO_2 released from the cycling of recently accumulated organic matter (and exudates) in the near-surface layer (Berglund & Berglund, 2008).

The annual CO₂ balance for BF is within the range of values reported for managed and restored (cool) temperate (and boreal) grasslands on organic soils (Table 8.1). GPP and ER were both higher than values reported for other sites, although comparable annual estimates of GPP (i.e. 1393 to 1719 g CO₂-C m⁻² yr⁻¹) have been reported for extensively grazed temperate grasslands on mineral soils (Jaksic *et al.*, 2006; Klumpp *et al.*, 2011). In most cases, the higher GPP at BF likely reflects a lack of biomass removal

by mowing, whereas higher ER is partly explained by greater contributions from autotrophic respiration. Despite higher annual GPP and ER, the annual NEE for BF in 2010 was similar to values reported by Nieveen *et al.*, (2005), Lloyd (2006) and at the extensively grazed Stein site (Veenendaal *et al.*, 2007), but significantly less positive than the range reported by Jacobs *et al.* (2007), and the intensively grazed Oukoop site (Veenendaal *et al.*, 2007) (Table 8.1).

Reference	Site description	NEE	GPP	ER
		$(g CO_2 - C m^{-2} yr^{-1})$		
This study	Bakers Fen - see site description	21.24±17.11	1634.99	1656.24
Nieveen <i>et</i> <i>al.</i> , (2005)	Rukuhia, Waikato, New Zealand. Intensive dairy farm from 1940s. Intensively grazed semi-natural grassland; 12 m peat depth; water levels -2 to -75 cm.	4.5		
Lloyd (2006)	Tadham Moor site, Somerset Levels, UK. Managed grassland on peat. Semi-natural mesotrophic grassland; <i>circa</i> 1.8m peat depth; water levels: <i>circa</i> 0 to -70 cm. Mown and grazed.	59 (NEP)		
Hendricks <i>et al.</i> , (2007)*	Horstemeer site, The Netherlands. Restored peat meadow (10 years under restoration). Semi-natural grassland; 2 m peat depth; Water levels: 0 to -40 cm; no biomass management.	-232 to -446	1156 to 1314	866 to 924
Jacobs <i>et al.</i> , (2007)	Assessment of four grasslands on organic soils. The Netherlands. Semi-natural grassland, under different management regimes and water level management regimes	220±90	1300±100	1520±30
Veenendaal et al. (2007)	Stein site, The Netherlands. Bird meadow nature reserve. Semi-natural grassland; 0.25 m peaty clay overlying 12 m eutrophic peat deposits. Ditch water levels: <i>circa</i> 60 to 80 cm. Mown and grazed.	-5.7	1539	1542
<i>et al.</i> (2007)	Oukoop site, The Netherlands. Intensively managed daily farm. Semi-natural grassland; 0.25 m peaty clay overlying 12 m eutrophic peat deposits. Ditch water levels: <i>circa</i> 60 to 80 cm. Mown and grazed, and fertilized with manure.	133.9	1460	1596
Herbst <i>et al.</i> , (2012)*	Skjern Meadows, Western Denmark. Restored former arable land. Drained in 1969, restored between 1999 and 2002. Semi-natural wet grassland. Peat depth unknown. Water levels unregulated. Mown and grazed.	-53 to -268		

Table 8.1: Summary of annual carbon dioxide budgets for managed and restored temperate and boreal fens with a permanent vegetation cover.

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Notes: References marked with a star are restored sites. NEP is net ecosystem production which includes losses of C via biomass removal. NEP values are only provided when no estimate of NEE was reported.

The annual NEE at BF contrasts strongly with other restored (temperate and boreal) fens, where strong annual CO2 sinks have been reported (Hendricks et al., 2007 and Herbst et al., 2012 in Table 8.1). In contrast to BF, these sites were restored from less intensive (i.e. pasture) land management (Hendricks et al., 2007) and/or shorter periods of productive land use (Herbst *et al.* 2012). The strong CO₂ sinks at these sites supports the suggestion that the CO₂ sink function is more likely to be reinstated at less degraded sites, where peat depth is greater and hydrological conditions more readily restored (Höper *et al.*, 2008). Subsequent research at the Horstemeer site showed that ER did not respond to changing water levels, as the associated changes in surface moisture content were not sufficient to significantly influence heterotrophic respiration rates (Parmentier *et al.*, 2009). This was clearly not the case at BF during 2010, where a large seasonal variation in surface moisture content (and ER) was observed (Figure 5.5).

Accumulated NEE was of similar magnitude (i.e. within the uncertainty range) at BF and WSF during the paired measurement period of 2010 (Tables 7.3 & 7.4). Interestingly, total GPP was higher at BF compared to WSF during this period, the difference mainly reflecting higher rates of spring photosynthesis at the regenerating site (Figure 7.6). At a first approximation, higher cumulative GPP (and ER) at BF appears somewhat counter-intuitive, given the much larger standing biomass (i.e. NPP) at WSF (i.e. compare Figures 4.4 & 4.5). However, this difference may reflect a higher C use efficiency of dominant species at WSF (i.e. lower autotrophic respiration demands), as well as differences in C allocation patterns (Rocha & Goulden, 2009). This would also part explain higher accumulated ER at BF. Measurements of NPP (i.e. Rocha & Goulden, 2009) and/or partitioning of ER into auto- and heterotrophic components would be required to test this hypothesis. A further potential explanation may relate to the presence of the grazing herd. Ward *et al.*, (2007), for example, showed that grazing activity served to increase both photosynthetic and respiratory fluxes at (upland) peatland environments in the UK.

8.1.6 Carbon cycle (CO₂) impacts of Fenland rehabilitation

On the basis of the annual CO₂ balance for BF and available estimates of CO₂ losses from arable fens (Chapter 2), it is possible to provide a first-order estimate of the CO₂ benefits of restoration in 2010 (Table 8.2). Using the CO₂ EF currently used to represent CO₂ losses for cultivated UK fens with peat depths less than 1 m (109 g C m⁻² yr⁻¹), a net CO₂ emissions reduction (i.e. an avoided loss) of -87.7±17.11g CO₂-C m⁻² y⁻¹ (-322.08±62.79 g CO₂ m⁻² yr⁻¹) is obtained for 2010. As noted previously (Chapter 2), estimates of CO₂ losses from arable fens have been poorly quantified and the true magnitude of CO₂ losses remains uncertain. If the higher CO₂ emissions estimate of Gauci (2008) is applied (320 g CO₂-C m⁻² yr⁻¹), the avoided loss increases to net reductions of -298.76±17.1 g CO₂-C m⁻² yr⁻¹ (-1096.45±62.79 g CO₂ m⁻² yr⁻¹).

Table 8.2: Estimates of CO_2 emissions reductions in 2010 calculated using data from BF in 2010 and available estimates of CO_2 losses from arable fens.

Area (hectares)	CO ₂ emissions reduction		
Estimated CO ₂ loss from arable fens	$1.09 \text{ Mg CO}_2\text{-C ha}^{-1} \text{ yr}^{-1}$	$3.2 \text{ Mg CO}_2\text{-C ha}^{-1} \text{ yr}^{-1}$	
1 ha	0.87	2.99	
Current Wicken Vision Project Area (390 ha)	336.69	1159.59	
Fens less with peat depth less than 1 m (126,000 ha)	108775.80	374635.80	

Notes: The value of 109 g CO₂-C m⁻² yr⁻¹ is from Bradley (1997). The value of 320 g CO₂-C m⁻² yr⁻¹ is from Gauci (2008). Tabulated values are provided in units of Mg CO₂-C m⁻² yr⁻¹.

Assuming the CO_2 flux measurements from BF (and values for arable fens) can be considered broadly representative of the 390 ha currently under restoration management within the Wicken Vision project area, a net CO₂ emissions reduction of 336.69 to 1159.59 Mg CO₂-C yr⁻¹ (1235.65 to 4255.70 Mg CO₂ yr⁻¹) is calculated for 2010 (Table 8.2). Hypothetical application of these values to the area of cultivated UK fen peat less than 1 m in depth (from Bradley, 1997) results in avoided emissions of 108776 and 374636 Mg CO₂-C yr⁻¹, depending on the value uses to represent CO₂ losses from arable fens (Table 8.2). On the basis of the values currently used to represent CO₂ losses from arable fens in the UK (Bradley, 1997; Choudrie *et al.*, 2009), this theoretical emissions reduction would represent a *circa* 21% CO₂ emissions reduction relative to the 137340 Mg CO₂-C yr⁻¹ currently reported for the 126,000 ha of shallow (<1 m) cultivated fenland, and a *circa* 6.4% reduction relative to the total CO₂ (445,500 Mg CO₂-C yr⁻¹) losses currently reported for all (shallow and deep) drained and cultivated lowland fens. However, as noted previously, the true magnitude of CO₂ losses from shallow peats is found to be lower (higher), then the CO₂ emissions reduction would clearly be reduced (increased).

The values presented above represent first-order estimates of potential CO_2 savings⁵⁴. They are based on limited data, both in terms of single year of data from BF (obtained during an atypical year – Chapter 5) and uncertain estimates of annual CO_2 losses from arable fens. In contrast to previous assessments (i.e. Natural England, 2010), however, these values are based on data obtained in the Fenland (and UK). It is stressed that the data from BF do not represent a UK (or East Anglian) CO_2 EF, but rather a first step towards developing such a value. As such, these estimates can be considered a

⁵⁴ The annual estimate of NEE does not represent an annual CO_2 EF, but a first stage towards estimating an annual EF. As noted in Chapter 2, the development of EFs requires data from multiple sites obtained over a five year period.

refinement to values currently used to represent CO_2 fluxes from UK fens. Further, these estimates only consider CO_2 fluxes. Measurements of other GHG fluxes are required to assess the contemporary climatic impact of restored fens in this region (see section 8.2.11).

The calculations of avoided CO_2 losses (above) are indicative of a relatively large (technical) potential for CO_2 emissions reductions following land conversion from arable to (less intensive) restoration management. However, given the agricultural economy (and culture) of the Fenland (Morris *et al.*, 2000; 2010), and in the absence of an appropriate market price for carbon or government policy to support taking intensive agricultural land on peat out of production, it is very unlikely that such widespread restoration activity will take place beyond existing restoration target areas (e.g. Morris *et al.*, 2000; Schaller, Kantelhardt & Drösler, 2011).

The data from BF in 2010 (and from WSF in 2009 and 2010) have implications for previous assessments of the CO₂ (and GHG) benefits of peatland restoration in the Fenland. On the basis of the (single) annual estimate presented in this study, it appears that the C benefits may be one of an avoided loss, and the achievable C (and GHG) benefits of restoration could have been overstated. For example, (the limited number of) previous assessments (Table 2.7) have commonly assumed that (i) the maintenance of high water levels across large targeted restoration areas is achievable; (ii) restoration will result in negative CO₂ emissions after some (variable) timeframe; and (iii) the CO₂ balance will ultimately come to approximate that of an undamaged fen after some (variable) time period (Table 2.7).

Conditions at BF in 2010 illustrate the technical challenges associated with peatland restoration in East Anglia (and elsewhere). In 2010, low spring and early summer rainfall, a warm midsummer period (i.e. high evaporative demand) combined with the shallow peat layer resulted in dry site conditions throughout most of the growing season. The (general) absence of peat-forming species (Stroh *et al.*, 2012), and presence of species more commonly associated with drier locations (i.e. agricultural grasses, *C. monogyna*), suggests the dry conditions observed during 2010 may be more broadly representative of this site. This implies that a more adaptive water management strategy is required if succession towards a mire flora is to be achieved (Haapalehto *et al.*, 2011), although this appears unlikely given the current system of water allocation rights.

In the longer-term, it is possible that water levels (at least at this location) could be more effectively managed due to buffering effects as more adjacent arable land comes out of agricultural production. However, projected trends towards warmer and drier summers (Table 8.3) may ultimately prove restrictive (i.e. higher evapotranspiration rates). Under the current management regime, it appears unlikely that renewed (and sustained) peat formation will resume at BF in the near-term. It is, however, possible that wet surface conditions could be more readily achieved in areas with deeper peat. Some (observational and rather circumstantial) evidence for this is provided at BF where areas of deeper peat are associated with wetter surface conditions. Restoration of deeper peats would also have a higher overall mitigation potential, since cultivation of these areas is associated with the highest CO_2 emissions (Bradley, 1997). Under current conditions, however, such areas are less likely to be considered for restoration as they are typically the most productive agricultural soils and contribute a large fraction of domestic food production (Morris *et al.*, 2000; 2010).

Climate variable	Central estimate	90% probability range	
Mean winter air temperature	+2.2°C	+1.1°C to +3.4°C	
Mean summer air temperature	+2.5	+1.2°C to +4.3°C	
Mean daily maximum air temperature	+3.4°C	+1.3°C to +6°C	
Mean daily minimum air temperature	+2.7°C	+1.2°C to +4.7°C	
Annual precipitation	0%	-5% to 5%	
Winter mean precipitation	+14%	+3% to +31%	
Summer mean precipitation	-17%	-38% to +6%	

Table 8.3: Projected changes in air temperature and precipitation for the East of England by the

 2050s under a medium greenhouse gas emissions scenario (Data source: UKCIP, 2010).

Notes: Positive values indicate an increase in the respective climatic variables; negative values denote a decrease.

In theory, highly degraded ex-arable fens could be managed as net CO_2 sinks (assuming water is not limiting). As the BF site was close to the CO_2 compensation point in 2010, a shift from a small net CO_2 source to a net sink would only require a small change in one or both of the CO_2 flux terms (i.e. GPP and/or ER). As noted above, the short period of net uptake following the recharge in soil moisture levels after high rainfall in August provides some evidence that the CO_2 sink period (and annual sink strength) could be extended if wetter surface conditions were maintained. Moreover, it remains

unclear if water abstractions during the autumn months would have been sufficient to tip the balance in favour of net CO_2 uptake. On the basis of the current (and still limited) dataset, however, it appears that values used in previous assessments (being of opposite sign and sometimes magnitude to the estimate of NEE for BF in 2010) may have overestimated the feasibility and mitigation potential of Fenland rehabilitation (see Table 2.7), at least in terms of sites with shallow residual peat layers.

The convergence of cumulative NEE at WSF and BF during the paired flux measurement period of 2010 resulted from large differences in seasonal CO₂ exchange dynamics (Figures 7.2 and 7.3 and discussed above). On the basis of the available data, it is not possible to determine whether the CO₂ balance of the BF site will respond similarly or dissimilarly to WSF in years with different environmental conditions (e.g. Klumpp *et al.*, 2011; Leppälä *et al.*, 2011). As such, it should not simply be assumed that the CO₂ balance of the regenerating fen will remain similar to that of the semi-natural (reference) site in other years, as could perhaps be inferred from the 2010 data.

Finally, the results from WSF show that relatively intact fens are not necessarily sinks for atmospheric CO_2 , as has often been assumed when estimating the (longer-term) impacts of Fenland rehabilitation (e.g. Gauci, 2008; Natural England, 2010). Although data limitations have been highlighted in previous assessments of the C (or GHG) benefits of peatland restoration in East Anglia, the results of this study emphasise the need to better constrain uncertainties. This is particularly important when estimates of potential C (or monetary) gains are presented in ways that could influence land management or political decision making (e.g. Gauci, 2008; Morris *et al.*, 2010; Natural England, 2010).

8.1.7 Implications for land management

The results presented in this study have implications for the management and long-term resilience of these managed peatlands in a region that is projected to experience considerable climatic change over the coming century (Table 8.3). In terms of WSF, the potential for large losses of C in the form of CO_2 are of major cause for concern, both in terms of CO_2 emissions to the atmosphere, and for the long-term resilience of this ecologically, historically and culturally important wetland. If climate change projections for this region are realised (Table 8.3), then it is likely that higher summer temperatures and decreased rainfall will result in large releases of C as CO_2 if low lateseason water levels become more common. On the other hand, a strong reduction in net CO_2 losses was observed following extreme late summer rainfall in 2010 (along with a short period of net uptake in September). Although representing an extreme climatic event, this natural experiment demonstrates the potential for reducing net CO_2 losses (or potentially enhancing the sink strength) by maintaining high water levels, particularly during the autumn months when photosynthesis is in decline.

The need to maintain high water levels at WSF echoes the conclusions of an ecohydrological study at the same site. Harding, Smith & Williamson (2005) concluded that summer water levels should not fall below -30 cm if the current vegetation cover is to be maintained. Whilst this would likely reduce GPP (Figure 6.12 & Table 6.4), the

results of this study show that seasons with higher assimilation are not necessarily associated with net CO_2 uptake (Figure 7.4). This confirms previous suggestions that peatland management should focus on reducing respiratory CO_2 losses (e.g. Rogiers *et al.*, 2008; Hatala *et al.*, 2012). The new wind pump at WSF (operational since 2011) may prove effective in maintaining these conditions, providing water rights do not prove limiting. Ongoing measurements at this site will be able to determine whether this intervention proves effective in preventing large CO_2 losses from WSF during dry periods (i.e. during a period of extended drought that affected southern England during 2011/12).

In terms of longer-term ecosystem resilience and management, it is worth noting that the sites investigated in this thesis represent successional stages (seres) in the transition towards native woodland (Godwin, 1936). At WSF, vegetation is currently maintained under steady-state management (rotational cutting), designed to maintain open fen habitat for its biological importance (Friday & Colston, 1997). Evidence from other peatlands highlights the role of diversity in plant functional types (i.e. increased production by shrubs/woody species) in offsetting heterotrophic CO_2 losses during dry periods (e.g. Riutta *et al.*, 2007a; Sulman *et al.*, 2010; Leppälä *et al.*, 2011; Flanagan & Syed, 2011). If it proves impracticable to maintain high water levels in the longer-term (i.e. under projected climate change), it is possible that suppression of successional processes could prove detrimental to the adaptive capacity of this peatland (in terms of C balance). However, as the true value of WSF (arguably) lies in its extremely high species diversity, every effort should be made to conserve the fen in its current state. The regenerating BF site (by definition) represents a transitional stage between arable land use and some (open-ended) 'recovery' state (Hughes *et al.*, 2011). As such, the data from 2010 represent a snapshot of an ecosystem that is developing along a potentially novel (and unpredictable) successional trajectory. Current site management aims to maintain open habitat (in this case a dynamic habitat mosaic) for species conservation objectives. As with WSF, if it proves difficult to maintain high water levels at this site (as appears to be the situation), it is possible that the current grazing regime could prove disadvantageous in terms of C balance. If this is the case, it could imply that the objectives of C-orientated land management and biodiversity conservation will not necessarily be as equally well-served by the same land management regimes. This highlights the need for longer-term monitoring at a range of space and time scales, as well as a need to quantify the impacts of grazing on the CO_2 (and overall GHG) balance of regenerating sites (e.g. Ward *et al.*, 2007; Baldocchi *et al.*, 2012).

It is important to recognise that the restoration of BF and the wider Wicken Fen Vision were primarily conceived for objectives of habitat (re)creation and biodiversity conservation (The National Trust, 2007). As Lloyd (2006) notes, any net C benefits must be weighed against the provision of other ecosystem services. Although the BF site continued to lose a small amounts of soil C as CO_2 in 2010, the (estimated) avoided loss represents an improvement compared with continued arable land use, at least in terms of slowing rates of peat loss and prolonging the longevity of associated habitats (although not necessarily in terms of the contemporary climatic impact). Thus, this reduction should be considered an additive benefit alongside observable increments in biodiversity (e.g. Stroh *et al.*, 2012; Hughes *et al.*, 2011) and the opening up of

previously restricted arable land for its amenity and tourism value (The National Trust, 2007).

As the CO_2 balance of BF was close to neutral in 2010, efforts to maintain permanently high water levels at this and other similar sites should be considered with care. Although wetter surface conditions at this site would (most likely) promote succession towards a mire community (assuming water is not a limiting factor) (Haapalehto *et al.*, 2011), higher water levels could potentially lead to high CH_4 (and N_2O) emissions (Baird, Holden & Chapman, 2009; Parmentier *et al.*, 2009). On the other hand, if the NEE for 2010 proves more broadly representative of the CO_2 balance of BF (and other regenerating fens in The Fenland), then the inevitable depletion of the remaining peat layer will not benefit any long-term stakeholder objective. Clearly, this highlights the need to quantify other GHG fluxes under different environmental conditions and management regimes, and requires efforts (i.e. modelling studies) to identify which (if any) management regimes are likely to be most beneficial in terms of overall ecosystem service provision.

8.2 Limitations and future research

As with all scientific studies, this research was characterised by a number of methodological and other (i.e. pragmatic) constraints. Whilst it is fundamental to recognise these limitations, it is equally important to recognise that many of these limits present avenues for ongoing and/or future research activity. The following sections identify limitations in the current research and, where relevant, suggest methodological

improvements and/or areas for extended research. In doing so, it should be noted that many of the issues identified are currently being addressed by a follow on PhD project, existing within the wider framework of a Defra-funded project on GHG fluxes from lowland UK peatlands (Defra project SP1210), and a National Environmental Research Council (NERC) Urgency Grant addressing CO_2 fluxes from cultivated lowland fens (Morrison *et al.*, submitted).

8.2.1 Calibrations

It was not possible to calibrate either of the Li7500 IRGAs at a desired frequency during this study (Appendix A). This institutional barrier represents the single greatest limitation to the quality of the flux measurements reported in this thesis. Future research would benefit from the availability of CO₂ calibration standards at the start and for the duration of a given measurement period (ideally traceable to World Meteorological Organisation standards) and regular (i.e. monthly) *in situ* calibrations. The acquisition of a portable dew point generator (i.e. the recommended LI-COR Li-610) for *in-situ* calibrations of Li7500 H₂O channels is strongly recommended. Additionally, although impractical here, comparative studies such as this would benefit from comprehensive cross-calibrations of all (EC and environmental) sensors; ideally, prior to and at regular intervals during deployment in the field.

8.2.2 Ancillary measurements and datasets

The full range of supporting environmental measurements was not available for both flux sites. For example, peat, temperature, volumetric soil moisture content and PAR were not measured at the WSF flux tower. To enable more effective analyses, future research would benefit from installing matched (i.e. identical and cross-calibrated) instrumentation at all sites used in comparisons.

MODIS EVI was used as a proxy for ecosystem phenology in this study. Future work would be improved by (regular) acquisition of phenological data (i.e. LAI, aboveground biomass) at field scale, either using direct measurements (i.e. LAI meter or destructive sampling) or tower mounted sensors (i.e. the SKR1800 series NDVI sensors, Skye Instruments, Llandrindod Wells, UK). Similarly, further research consideration of other factors influencing CO_2 exchanges, such as seasonal between-site differences in (soil and plant) nutrient dynamics (e.g. Glenn *et al.*, 2006; Flanagan & Syed, 2011), and differences in soil organic carbon content. Smaller-scale (i.e. chamber) flux measurements could also be used to compliment EC measurements (discussed below).

8.2.3 Energy balance closure

It was not possible to close the surface energy budget at either of the flux measurement sites (Chapter 4). The near-ubiquitous lack of full EBC remains an important, challenging and open research problem for the micrometeorological and ecosystem flux measurement communities (Foken *et al.*, 2011). Future research could aim to explore reasons for the lack of EBC (Table 3.3), as well as the potential implications for CO_2
flux measurements and derived CO_2 budgets. Improved consideration of the reliability of soil heat flux measurements (and storage terms) and the heterogeneity of the measurement source areas (particularly at BF) would likely be the most appropriate starting points.

8.2.4 Data handling and analysis methods

This study used standardised methods of data processing, data gap-filling and flux partitioning (Chapter 4). Alternative data handling protocols could potentially prove more effective in estimating NEE at these peatland environments. For example, variants of a number of the analysis methods used in Chapter 6 could be used for data gap-filling and flux partitioning (i.e. light and temperature responses, regression models). Future work could explore which (if any) methods provide best results for these environments, and to quantify any bias introduced by such procedures (e.g. Falge *et al.*, 2001; Moffat *et al.*, 2007; Desai *et al.*, 2008). Similar assessments could be used to further explore the influence of other data handling procedures (i.e. QC) on measured fluxes and derived CO_2 budgets.

Correlation and regression analysis were used to explore the factors influencing land/atmosphere CO_2 exchanges (Chapter 6). Although these methods were sufficient for addressing the questions posed by the current work, such analyses become significantly improved using multi-year datasets (e.g. Griffis *et al.*, 2000; Aurella *et al.*, 2004; Sottocornola & Kiely, 2010; Flanagan & Syed, 2011). Moreover, it is noted that the analytical methods used in this study are only valid under the conditions of the data

used in the regressions. The use of process-based models would be desirable to better diagnose and/or predict CO_2 exchange dynamics, (i.e. interactions/feedbacks between assimilatory and respiratory processes, and interactions/feedbacks between energy, water and C fluxes). Although the extent of fenland restoration remains limited (at least at the current time), development (or calibration) of process-based models, would represent a first step towards meeting the requirements of Tier 3 GHG emissions accounting (IPCC, 2006; Smith *et al.*, 2012).

8.2.5 Winter measurements at Wicken Sedge Fen

 CO_2 flux measurements were not obtained during the cold winter and early spring periods at WSF (i.e. 1st January to 19th March). As such, an estimate of the annual CO_2 exchange was not provided here⁵⁵. It was previously noted that net CO_2 losses at WSF between January and 19th March would likely have rendered the site CO_2 neutral or a small net source in 2010 (and a larger source during 2009). EC measurements are ongoing at both of these flux measurement sites (Pan *et al.* 2012) and will aim to capture CO_2 (and other C) fluxes over a number of complete annual cycles to better determine the CO_2 source/sink status of these sites.

8.2.6 Temporal representativeness

This thesis reported CO_2 fluxes obtained over a short measurement period. As such, the results of this study are only representative of the conditions under which the

⁵⁵Attempts to model CO₂ exchange using data either side of the long data gap resulted in unrealistic estimates (e.g. notable step changes) when plotted as daily averages.

measurements were obtained. The results from WSF and other peatland studies (e.g. Shurpali *et al.*, 1995; Bubier *et al.*, 2003; Cai *et al.*, 2010) demonstrate CO_2 (and other) exchange processes are strongly influenced by interannual variations in environmental conditions. It is very unlikely that the CO_2 budgets presented in this study reflect the true magnitude of (seasonal or annual) NEE at these study sites. By way of example, Figure 8.1 compares monthly temperate and precipitation observations during the measurement period against monthly values for 2011 and (part of) 2012. In brief, 2011 was characterised by warmer than average spring and autumn conditions, a cooler than average summer, and a state of extreme drought. In contrast, 2012 experienced extreme spring drought, followed by some of the wettest summer months on record. Both years experienced significantly milder winter conditions than 2009 and 2010.



Figure 8.1: Comparison of monthly average air temperature and precipitation during the measurement period against conditions in 2011 and 2012. Plots show (a) monthly average air temperature; (b) total monthly precipitation; (c) monthly temperature anomalies (d) monthly precipitation anomalies; and (e) cumulated monthly precipitation. Temperature data are from Cambridge NIAB. Precipitation data are from the Met Office rain gauge in Stretham. Temperature and precipitation anomalies were calculated using the 1979 to 2008 baseline (as in chapter 5). Data supplied by the Met Office.

The observed variability in weather conditions since the end of the data collection phase of this thesis (Figure 8.1) will undoubtedly have strong implications for CO_2 (and other GHG) exchanges at the measurement sites. On the basis of the findings of this research, it is likely that warmer winters and extended drought conditions would serve to enhance net CO_2 losses from WSF, whereas the CO_2 sink strength would most probably be enhanced during warmer spring conditions and the extremely wet conditions of summer 2012. Measurements obtained during these contrasting conditions will provide insight into the variability in NEE. In particular, measurements obtained during the extremely wet conditions of 2012 will provide information on the influence of high water levels⁵⁶ on the CO_2 balance of the regenerating site. This large variability in weather conditions over a short period serves to underline the need for longer-term measurements in order to better quantify the variability in NEE at these (and other) peatland sites.

8.2.7 Spatial heterogeneity

Spatial heterogeneity in CO_2 fluxes was not addressed in this research. EC measurements provide spatially-integrated measurements at ecosystem scale, but do not provide information on flux dynamics at space scales below that of the tower footprint (Laine *et al.*, 2006; Teh *et al.*, 2011). Small-scale chamber studies show peatland gaseous C exchanges show large spatial (and temporal) variability (e.g. Bubier *et al.*, 2003; Becker *et al.*, 2009; Cai *et al.*, 2010; Teh *et al.*, 2010). Furthermore, the spatial arrangement of communities within a given area strongly influences gaseous C exchanges at landscape-scale (Laine *et al.*, 2006; Riutta *et al.*, 2007a; 2007b; Becker *et al.*, 2009). At BF in particular, it is likely that the heterogeneity of the site may have

⁵⁶ Although no water level data were available at the time of writing, field observations at the site in July 2012 found that water levels were at or above the fen surface at this time.

biased the flux measurements under some atmospheric (i.e. footprint) conditions (Herbst *et al.*, 2012).

Future work at these measurement sites would benefit from smaller scale CO₂ (and non-CO₂) chamber flux measurements combined with more comprehensive footprint modelling than was used in this study (e.g. Schrier-Uijl *et al.*, 2010; Laine *et al.*, 2006; Riutta *et al.*, 2007b). Such measurements could help identify the most appropriate land management interventions and/or target communities for reduced CO₂ loss/enhanced uptake at these sites, and whether (or not) such measures are compatible with other land management objectives (i.e. biodiversity conservation). Nocturnal chamber measurements could provide datasets for (i) validating nocturnal EC measurements (Goulden *et al.*, 1996; Reichstein *et al.*, 2005a; Smith *et al.*, 2010a); and (iii) separating auto- and heterotrophic components of the total respiratory efflux (discussed below).

8.2.8 Spatial representativeness

The high costs of EC systems necessarily limit the application of the technique to a small number of fixed locations. Clearly, this raises issues of replication (Schrier-Uijl *et al.*, 2009) and questions on the representativeness of the study sites relative to other (similar) ecosystems. For example, both sites reported here have an ecology and soil characteristics determined by historical land management practices and site conditions (i.e. position in the landscape, hydrology), modulated by current land management activities (i.e. mowing, grazing, regulation of water levels). It is therefore uncertain how

well the flux measurements reported here represent the CO_2 exchange dynamics of other semi-natural, managed or restored fens in this region (and beyond), or even whether process knowledge can be extrapolated to sites with different vegetation types and management regimes.

At restored sites in particular, the trajectory of ecosystem development (and associated flux dynamics) will be influenced by starting conditions (Höper *et al.*, 2008), which in turn will reflect diversity in past agricultural land use (e.g. Kutsch *et al.* 2010). Further work is needed to assess the representativeness of the study sites relative to other semi-natural and restored peatlands, ideally supported by additional flux measurements. Future work at non-grazed locations is needed to determine the influence of the grazing regime. Measurements at less degraded restoration sites with deeper peat layers are required.

8.2.9 Partitioning the respiratory efflux

EC does not provide information on factors influencing autotrophic and heterotrophic contributions to ER (Reichstein *et al.*, 2005a; 2012). This is significant, since only the heterotrophic release of historically accumulated (i.e. old) soil C directly influence atmospheric C loading and climate change⁵⁷ (Berglund & Berglund, 2008; Page *et al.*, 2011). Improved understanding of respiration dynamics would be gained by attempts to partition the respiratory efflux using smaller-scale chamber flux measurements (e.g. Jauhiainen *et al.*, 2011) and/or isotopic techniques (e.g. Kuzyakov, 2006). At BF, areas

 $^{^{57}}$ CO₂ losses to the atmosphere via autotrophic respiration are climatically inert as they reflect the release of CO₂ from recently fixed photosynthates.

of bare peat could potentially be used for such purposes, although careful consideration of the influence of livestock (i.e. via faeces and urea deposition) is clearly required at grazed sites.

8.2.10 CO_2 emissions from a able fens

The annual CO_2 balance from the BF site provides the first empirically-derived evidence for a net CO_2 emissions reduction following arable fen restoration in East Anglia. However, this reduction was calculated on the basis of the best (currently) available estimates of annual CO_2 (or more correctly CO_{2-e}) losses from arable fens (Bradley, 1997; Gauci, 2008). These values were estimated on the basis of peat subsidence rates and modelling and not direct CO_2 flux measurements. These estimates are therefore uncertain due to uncertainties relating to: (i) the fraction of subsidence attributable to oxidation; (ii) the proportion of C transported via fluvial and aeolian pathways; and (iii) the interannual variability in C loss rates. The appropriateness of these values, and therefore the estimates of net CO_2 emissions reductions attributed to restoration in 2010, requires further refinement.

The magnitude of CO_2 (and other C and GHG) emissions from cultivated fens in East Anglia (and their spatial and temporal variability) has been identified as one of the largest uncertainties in terms of the UK peatland (and land C) balance (Worrall *et al.*, 2011; Evans *et al.*, 2011). At the time of writing, this data gap is being addressed by EC measurements at an intensively cultivated fen in the Norfolk Fens (Morrison *et al.*, submitted). These new data will provide an improved estimate of the magnitude of CO_2 losses from arable fens, providing a more robust foundation for estimating the C benefits arising from peatland rehabilitation. Preliminary results show a loss of *circa* 300 g CO₂-C m⁻² over a 110 day measurement period, although this estimate was obtained at a site with a deeper peat layer than is present at the BF restoration site. Measurements of aeolian C transport are underway at the same arable peatland.

8.2.11 Other carbon and greenhouse gas fluxes

This study only considered only considered land/atmosphere CO₂ exchange. Full C and GHG gas accounting requires quantification of vertical fluxes of CH₄, the magnitude and fate of any fluvial and aeolian gains/losses of C (Billett *et al.*, 2010; Dinsmore *et al.*, 2010) as well as emissions of N₂O (Hendricks *et al.*, 2007). At both sites, the seasonal (at WSF) and annual CO₂ balances were either positive (WSF in 2009) or close to CO₂ neutral (WSF in 2010 and BF in 2010). As such, other C losses and emissions of more potent biogenic GHGs (CH₄ and N₂O) are likely to have a strong influence on the contemporary C balance and climatic impact of these managed peatlands (e.g. Teh *et al.*, 2011). By way of example, emission of only 3.3 g CH₄ m⁻² yr⁻¹ would nullify the cooling influence of the estimated CO₂ removal (of -22.66 g CO₂-C m⁻² or -83.16 g CO₂ m⁻²) at WSF during the 2010 measurement period, and would serve to increase the (contemporary) radiative impact of WSF and BF in 2009 and 2010, respectively.

It is likely that CH_4 emissions are seasonally high at both sites during warm periods with high water levels, such as spring periods when labile plant residues and root exudates are decomposed under waterlogged conditions (Brix, Sorrell & Lorenzen, 2001). It also possible these sites may act as a net CH₄ sink during dry periods (Maljanen *et al.*, 2004; 2007). At WSF, however, CH₄ transport via deep-rooted 'shunt' species (i.e. *P. australis*) could also be effective in maintaining CH₄ emissions during dry periods (Brix, Sorrell & Lorenzen, 2001; Couwenberg *et al.*, 2011). At both sites, it is likely that CH₄ emissions are high from emissions 'hotspots', such as permanently inundated ditch communities (Hendricks *et al.*, 2007; Becker *et al.*, 2008; Teh *et al.*, 2011; Page *et al.*, 2011; Carter *et al.*, 2012). At BF, the presence of the grazing herd represents a further (mobile) CH₄ source that should be accounted for (Herbst *et al.*, 2011; Baldocchi *et al.*, 2012). Similarly, N₂O emissions may be locally high at BF due to microbial processing of faeces and urea during periods of intermediate and/or fluctuating soil moisture (Couwenberg *et al.*, 2008; Couwenberg, 2011).

Personal field observations made throughout the study period during visits to these sites do not suggest that fluvial C transfers (e.g. DOC/POC) are an important component of the C balance at either fen. In particular, fluvial C *exports* are unlikely to be a significant component of the C balance at the hydrologically isolated BF site. This assumption will be tested empirically at both fens during 2013 (Pan *et al.*, 2012). Fluxes of all C and GHGs are currently being addressed at the WSF and BF sites as part of the Defra project on lowland peatlands (Defra project SP1210). Future research should aim to capture the full spectrum of C and GHG dynamics prior to, during and after the transition from arable land use to restoration management (discussed below).

8.2.12 Land use transitions

The results from BF were obtained at a site that had been under restoration management for sixteen years at the time of measurement. Although space-for-time substitutions (i.e. chronosequences along land use gradients) provide insight into the C (and GHG) dynamics resulting from land use changes, an improved (longer-term) experimental design would be measurements obtained prior to, during and after the transition from one management regime to another (Evans *et al.*, 2011; Smith *et al.*, 2012). Such campaigns could mitigate some of the issues relating to differences in environmental conditions between spatially disparate sites, although issues of wider spatial representativeness would clearly remain (discussed above).

Measurement campaigns capturing land use transitions could account for short-lived, but potentially significant emissions events, such as enhanced CO_2 capture during revegetation (Höper *et al.*, 2008), and/or pulse emissions of non-CO₂ GHGs upon rewetting (Gauci, 2008). These events should be quantified and attributed to land use transitions in land-based GHG accounting (Couwenberg *et al.*, 2008; 2011). With large areas coming out of arable production in the Fenland (and elsewhere), future research should exploit the opportunity to capture such transitional GHG exchange dynamics.

8.2.13 Regionalisation/upscaling of fluxes

A final potential area for future (i.e. longer-term) research is the spatial modelling of CO_2 (and other GHG and energy) fluxes across the Fenland. Such analyses have been conducted for a number of regions by combining EC datasets, land cover (i.e. remotely-

sensed) information and land surface models (e.g. Papale & Valentini, 2003; Reichstein *et al.*, 2007; Xiao *et al.*, 2012). Longer-term and more spatially-comprehensive measurements are needed before such an analysis could be considered robust. Flux measurements for arable fens across a range of soil conditions (including mineral soils), crop types and management regimes would be required. Such an analysis would necessitate comprehensive efforts to characterise environmental conditions (i.e. edaphic, hydrological, ecological, land management practices, etc.) across the region (e.g. Smith *et al.*, 2012). Predictive modelling would necessitate assumptions on future drivers (i.e. social, political, cultural and economic) and trajectories of agricultural land management and restoration activity.

Conclusions

This research aimed to significantly improve current understanding and knowledge of the dynamics and magnitude of land/atmosphere CO_2 exchange at semi-natural and regenerating fens in East Anglia. The seasonal pattern of NEE at two managed fens was quantified and an analysis of the main factors influencing land/atmosphere CO_2 exchange presented. Time-integrated CO_2 budgets were provided for the two managed peatlands.

The new data presented in this thesis add to current knowledge on peatland C cycling by providing two of only three micrometeorological studies conducted at any type of lowland fen in the United Kingdom. The results from the BF site represent one of only two studies to have addressed CO_2 fluxes at a fen that has been restored after a long history of *arable* land use, and the first such measurements for the United Kingdom or temperate Europe.

The semi-natural Wicken Sedge Fen site functioned as a net source of 85.47 ± 25.78 g CO₂-C m⁻² (313.67±94.61 g CO₂ m⁻²) between 19th March and 31st December 2009 and a small net sink of -22.66±18.85 g CO₂-C m⁻² (-83.16±69.18 g CO₂ m⁻²) during the corresponding period of 2010. Gross primary production and ecosystem respiration were both enhanced during warm and dry conditions in 2009 compared to generally cooler and wetter conditions in 2010. In 2009, higher rates of photosynthesis during warm spring conditions were outweighed by high rates of net CO₂ loss during warm and dry conditions, whereas respiratory CO₂ losses were reduced following a rise in water levels during a period of extreme late summer rainfall. These results demonstrate the sensitivity of temperate fens to meteorological and hydrological variability. At the local scale, these results highlight the importance of maintaining high water levels to prevent large CO₂ losses from this internationally important wetland.

The results from the regenerating former arable fen represent the first quantitative estimate of a net CO₂ emissions reduction following restoration from intensive arable production in East Anglia. The BF site functioned as a small net source of 21.24 ± 17.11 g CO₂-C m⁻² yr⁻¹ (77.95±62.79 g CO₂ m⁻² yr⁻¹) in 2010. On the basis of the current values used to represent CO₂ emissions from drained and cultivated fens in the United Kingdom, this represents an avoided loss of -87.7 ± 17.11 g CO₂-C m⁻² y⁻¹ (or -322.08 ± 62.79 g CO₂ m⁻² yr⁻¹) compared to continued arable land use. Improved

quantification of carbon fluxes at cultivated and restored fens is required to refine this estimate.

A single year of measurements is not sufficient to determine the variability in the annual CO_2 source/sink status of the regenerating fen. Longer-term measurements capturing a wider range of environmental conditions are required to determine whether restoration management can prove effective in transforming agriculturally degraded fens in this region into net sinks for atmospheric CO_2 . On the basis of the 2010 data for this site, it appears that more adaptive hydrological management will be required if the abiotic conditions required for peat formation are to be achieved. Further measurements are necessary to better quantify the potential response of the CO_2 balance to management interventions and under a broader range of environmental conditions.

The results of this thesis highlight the need for longer-term monitoring at these and other lowland peatland environments. Future studies aiming to measure and model CO_2 dynamics at peatlands in this region are needed, ideally capturing transitions from arable to restoration management and beyond. In order to fully account for the contemporary and future role of managed lowland peatlands within the C cycle, ongoing research should aim to better quantify the drivers, and the spatial and interannual variability in land/atmosphere CO_2 exchanges. Measurements of other climatically relevant carbon and greenhouse gas fluxes are in progress, and will better quantify the contemporary climatic influence of managed peatlands in The Fenland.

Appendix A: Li-7500 Calibrations

This appendix provides details of the calibrations and associated corrections applied to concentration measurements made using the Li-COR Biosciences Li7500 H_2O/CO_2 gas analysers used at Bakers Fen (BF) and Wicken Sedge Fen (WSF). As noted in Chapter 4, institutional constraints precluded the calibration of the IRGAs at a desired frequency over the course of this project. At both sites, a number of span (gain or slope) calibrations were considered unreliable and were not accepted. Calibration coefficients were reset to previous calibration settings values during post-processing for these periods using a correction factor (C.F).

Drift corrections were applied to adjust Li7500 CO₂ and H₂O concentration measurements between accepted (span) calibrations. The zero (offset) settings remained stable and no adjustments were applied. Corrections were applied by calculating sensor drift (S.D) for each thirty minute period between accepted calibrations using linear regression. (C.F.s and S.D. values were calculated as the ratio of the old to new span settings, i.e. C.F or S.D = old/new). Thirty minute sensor drift values were imported into the EdiRe software package using a pre-processed data file, and were applied to concentration measurements prior to other flux computations. For time periods when span calibrations were unreliable, the linear correction was applied after the respective C.F. adjustment.

A.1 Bakers Fen calibrations

Table A1 provides the calibration coefficients and correction factors for the BF site. The H₂O channel was calibrated using facilities at CEH, Wallingford on 11^{th} January 2010, 20^{th} March 2010 and 11^{th} January 2011. In all cases, the zero setting was reset using dry CO₂ free air. The span setting was set using a LI-COR Li-610 Portable Dew Point Generator. All H₂O calibrations at Wallingford were considered reliable and accepted. Linear drift corrections were applied between accepted calibrations. A further attempt was made to calibrate the H₂O channel settings at the University of Leicester (UoL) on 21^{st} May 2010 using synthetic air (zero H₂O and CO₂ standard, AirLiquide, UK) for the zero setting, and a Dew Point Hygrometer for the span setting. The span setting was reset to

the original value during post-processing until 15th July 2010 (11:00 am), when the original values were reset in the Li7500 control box.

Attempts to calibrate the Li7500 CO₂ span settings on 11th January and 20th March 2010 at Wallingford were considered unreliable as span settings showed an unrealistic decrease compared to previous values. CO₂ concentration measurements following these dates were set to previous settings during data post processing (using C.F. values in Table A1). Certified (to \pm 1%) zero CO₂ and H₂O in air, and 450 ppm CO₂ in air calibration standards were obtained in late May 2010 (AirLiquide, Birmingham, UK). Calibration of the CO₂ channel on 21st May 2010 at the UoL indicated sensor drift of 1.34% relative to factory settings, supporting the poor quality (i.e. set too low) of previous calibration attempts. A final calibration of the CO₂ channel was conducted following the close of the measurement period on 12th January 2010 using the certified standards (drift of 2.67%). Linear drift corrections were applied between accepted calibrations made using the certified standards. It is noted that more frequent calibrations would have been desirable; however, the small size of the gas standards limited the number of calibrations that could be performed.

Data	H ₂ O Channel					CO ₂ channel				
	zero	span	C. F.	S. D.	-	zero	span	C. F.	S. D.	
9.10.2010 to 15.01.2010	0.9339	0.9946			-	0.8891	0.9987			
15.01.2010 to 16.03.2010	0.9394	1.012		1.0175		0.8884	0.9345	1.0687		
20.03.2010 to 21.05.2010	0.94	0.9955				0.8888	0.9546	1.0462	1.0134	
21.05.2010 to $15.07.2010^+$	0.9405	0.9744	1.022			0.8887	1.0121			
15.07.2010 to 11.01.2011 [†]	0.94	0.9955				0.8887	1.0121			
11.01.2011	0.9405	1.0433		1.0480		0.8917	1.0391		1.0267	

Table A1: Calibration coefficients and correction factors used at the Bakers Fen flux measurement site.

Notes: Zero and span are the offset and gain settings of the Li7500; C.F. is the correction factor used to adjust concentration measurements to previous settings when calibrations were unreliable; S.D. denotes sensor drift between accepted calibrations. Values marked with a * are those when CO_2 span setting was unreliable and not accepted (and set to previous values using the respective CO_2 C.F. for the time period indicated). The time period marked with a + denotes the period when the H₂O span setting was unreliable after attempted calibration at the UoL (and set to previous values using the respective H₂O C.F. for the time period indicated). The period marked with a † indicates the period when the H₂O settings were reset to the previous values in the Li7500 control box (i.e. when the researcher gained the experience to identify the issue, and to avoid applying the correction in post-processing). S.D. corrections were applied between the first dates indicated by in the row following the previous drift correction.

A.2 Wicken Sedge Fen calibrations

Calibration coefficients and corrections factors used at WSF in 2009 and 2010 are provided in Table A2. The site operator removed the Li7500 from the WSF site for calibration in January 2010. The sensor was recalibrated on 25^{th} January at CEH, Wallingford (by the site operator), and replaced in late February (exact date unknown). As for BF, the H₂O channel calibration was considered reliable, although the CO₂ settings were not. The linear drift correction was applied to H₂O concentration measurements in 2009, but was small at *circa* 1.5% (Table A2). The CO₂ concentration measurements were set to original factory settings during the 2010 measurement period. The CO₂ channel of the Li7500 was calibrated using the certified gas standards on 19th January 2011 (i.e. cross-calibrated with the BF site), indicating total sensor drift of *circa* 2.2% from factory settings over the measurement period. The linear correction was applied to all 2009 and 2010 CO₂ concentration measurements. It was not possible to calibrate the H₂O channel of the WSF Li7500 at this time, and this limitation to the accuracy of the measurements is acknowledged.

Data		H ₂ O Channel				CO ₂ channel			
Date	Zero	span	C. F.	S. D.	-	zero	span	C. F.	
3.2009 to 25.02.2010	0.8675	0.991		1.0150	-	0.9216	0.9969		
2.2010 to 19.01.2011*	0.8702	1.0059				0.924	0.9598	1.0387	
01.2011						0.9241	1.0218		

Table A2: Calibration coefficients and correction factors used at the Wicken Sedge Fen flux measurement site.

Notes: Zero and span are the offset and gain settings of the Li7500; C.F. is the correction factor used to adjust concentration measurements to previous settings when calibrations were unreliable; S.D. denotes sensor drift between accepted calibrations. Values marked with a * are those when CO_2 span setting was unreliable and not accepted (and set to previous values using the respective CO_2 C.F. for the time period indicated). S.D. corrections were applied between the dates indicated in the date column.

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