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# CO<sub>2</sub> exchange and Carbon balance in two grassland sites on eutrophic drained peat soils

**E. M. Veenendaal<sup>1</sup>, O. Kolle<sup>2</sup>, P. A. Leffelaar<sup>3</sup>, A. P. Schrier-Uijl<sup>1</sup>,  
J. Van Huissteden<sup>4</sup>, J. Van Walsem<sup>1</sup>, F. Möller<sup>1</sup>, and F. Berendse<sup>1</sup>**

<sup>1</sup>Nature Conservation and Plant Ecology group, Wageningen University, Droevendaalse steeg 3a 6708 PD Wageningen, The Netherlands

<sup>2</sup>Max Planck institute for Biogeochemistry, Hans Knöll Straße 10D–7745, Jena, Germany

<sup>3</sup>Department of Plant Production Systems, Wageningen University, P.O. Box 430, 6700 AK Wageningen, The Netherlands

<sup>4</sup>Free University, Department of Hydrology and Geo-Environmental Sciences, Faculty of Earth and Life Sciences, Boelelaan 1085, 1081 HV Amsterdam, The Netherlands

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Correspondence to: E. M. Veenendaal (elmar.veenendaal@wur.nl)

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## Abstract

In this study we investigated the role of intensive and extensive dairy farm practices on CO<sub>2</sub> exchange and the carbon balance of peatlands by means of eddy covariance (EC) measurements. Year long EC measurements were made in two adjacent farm sites on peat soil in the western part of the Netherlands. One site (Stein) is a new meadow bird reserve and is managed predominantly by mowing in June and August. The second site (Oukoop) is an intensive dairy farm.

Minimum ecosystem flux of the grass sward (range  $-2$  to  $-34 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) showed a close and similar linear relationship with Leaf Area Index (LAI; range 1 to 5) except in maturing hay meadows, where minimum ecosystem flux did not decrease further. Apparent quantum yield varied between  $-0.02$  and  $-0.08$  (mean  $-0.045$ )  $\mu\text{mol CO}_2 \mu\text{mol}^{-1}$  photons at both sites and was significantly correlated with LAI during the growth season. Ecosystem Respiration at 10°C ( $R_{10}$ ) calculated from the year round data set was  $3.47 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  at Stein and  $3.64 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  at Oukoop.

Both sites were a source of carbon in winter and a sink during summer, with net ecosystem exchange varying between 50 to 100 mmol CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup> in winter to below  $-400 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$  in summer. Periodically both sites became a source after mowing. Net annual ecosystem exchange (NEE) for Stein was  $-8.4 \text{ g C m}^{-2} \text{ a}^{-1}$  and for Oukoop  $122.4 \text{ g C m}^{-2} \text{ a}^{-1}$ , the difference between the sites was mainly due a difference in GEP ( $101 \text{ g C m}^{-2} \text{ a}^{-1}$ ). However when biomass removal, manure applications and estimates of methane emissions are taken into account, both eutrophic peat meadows are a strong source for C ( $462 \text{ g C m}^{-2} \text{ a}^{-1}$  and  $465 \text{ g C m}^{-2} \text{ a}^{-1}$  at Stein and Oukoop, respectively).

## 1 Introduction

Peatland ecosystems cover approximately 5% of the total European land surface and have since the last ice age evolved as globally important sinks and stocks of carbon,

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storing up to one third of the terrestrial C pool (Gorham, 1991; Clymo et al., 1998). For many northern peatland ecosystems a sink strength has been demonstrated with a variety of measurement techniques including chamber flux measurements, radio carbon dating and micrometeorological techniques (Arneth et al., 2002; Schulze, 1999; Nykänen et al., 1995; Trumbore et al., 1999)

However, drainage and agricultural management can turn agro-ecosystems on peat soils from sinks into significant sources of carbon due to the high soil respiration rates (Armentano, 1980). Subsidence of peat soils in agricultural areas has long ago been recognised and attributed to the oxidation of the peat substrate. C loss rates from exploited agricultural ecosystems on peat soils have on decadal time scales been calculated to be in the order of  $2$  to  $3 \times 10^3$  kg C ha<sup>-1</sup> a<sup>-1</sup> (Schothorst, 1977; Wolf and Janssen, 1991; Franken et al., 1992). The separation of soil shrinkage effects from peat oxidation beckons caution and carbon losses from peatlands need more accurate assessment (Byrne et al., 2004).

Eddy covariance techniques allow for the spatial integration of CO<sub>2</sub> fluxes at landscape scales (Moncrieff et al., 1997) and are now commonly applied to measure the contemporary CO<sub>2</sub> exchange in terrestrial peatland ecosystems. Results from these measurements for peatland agro-ecosystems may be variable. For instance Hensen and co-workers (Hensen et al., 1995; Langeveld et al., 1997) found for an agricultural area with clay on peat soils in the central part of the Netherlands annual CO<sub>2</sub> emissions in the order of 300 kg C ha<sup>-1</sup> a<sup>-1</sup>. However, their measurements were made over discontinuous periods and are therefore potentially prone to large error (Alm et al., 1999). Also a detailed insight into the management practices in agricultural ecosystems is essential for the estimate of the carbon balance and its sink strength or lack thereof (Soussana et al., 2004; Vuichard et al., 2007).

Comprehensive measurements of the sink strength of managed grasslands on peat soils have recently been reported from New Zealand (dairy farm with rotational grazing; Nieveen et al., 2005) and the United Kingdom (hay production and late summer grazing; Lloyd, 2006) with estimates for annual net ecosystem exchange (NEE) losses

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ranging from 45 kg C ha<sup>-1</sup> a<sup>-1</sup> to 590 kg C ha<sup>-1</sup>, respectively. However, when grazing and biomass removal were included, net losses were estimated to be 1061 kg C ha<sup>-1</sup> a<sup>-1</sup> for the New Zealand site, but did not change for the UK site due to the minimal C removal there. This observation emphasises the importance of management practices on the C-budget, but comparisons between spatially separated sites may be confounded by climatic variation. Perhaps the best approach is then to compare areas that are in close proximity but differ in management.

In the Netherlands, fen meadow areas cover large areas in the west and North of the Rhine Delta and in some, meadow bird reserve establishment has led to less intensive farm management. This less intensive management can be contrasted to intensive dairy farming practices under the same climatic conditions. The objective of this study has been to assess these management systems in two adjacent fen meadow areas in the West of the Netherlands. We hypothesize, that both sites are a source for CO<sub>2</sub>, due to the high respiration rates of drained peat soils, but that extensive management practices will cause smaller total losses due to reduced exploitation of the vegetation.

## 2 Methods

### 2.1 Sites description

The experimental fen meadow sites were located near the town of Reeuwijk (Fig. 1). The climate is temperate and humid with mean annual precipitation of about 793 mm and annual long term mean temperature of 9.8°C.

The main wind direction is South West. About 20% of the area is open water (ditches or low parts in the landscape). Soils typically consist of a clayey peat or peaty clay layer of up to 25 cm on up to 12 m eutrophic peat deposits formed in the past by alder carr forest and/or reeds and sedges vegetation. Former pure peat deposits to the North West have been exploited for fuel and the area forms part of the Reeuwijk lake district. The Micrometeorological masts (height 3.05 m) were located in the Polder

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area Stein and Oukoop (Coord. 52°01'07.41" N" 04°46'43.49 E" and 52°02'01.16" N" 04°46'49.59" E), with contrasting management. The terrain is flat. The locations were chosen as to provide homogeneity in the expected footprint area (Anthoni et al., 2004; Rebmann et al., 2005). The masts were placed in areas, where the mean elevation of the polder is between 1.6 and 1.8 m below New Amsterdam Reference water level (NAP; also referred to as sea level). Ditch water level in the polder is being kept at -2.39 m NAP in winter and -2.31 m NAP in summer.

The polder Stein has become a meadow bird reserve, owned by the State Forestry Service and therefore presently under less intensive management. During the period of study, most parcels of land were in use as hayfields, which are mown twice after the 15 June and then sometimes grazed for a short period by livestock, which stay in the parcels day and night. A few parcels are being grazed for the whole summer period. Most land has been taken out of intensive production gradually over a period of about 20 years but the parcels within the mast footprint were acquired between 2000 and 2004. Average C and N content in the top 20 cm of the soils is 15% and 1.3%, respectively. The micrometeorological mast was surrounded by a free area of 500 m except in the North, where at a distance of 40 m, a 3 m high row of alder bushes exists as well as a house 450 m away from the mast in the same direction. No effects of these features were later noticed in the resulting EC measurements with wind from the North. In most parcels rye grass (*Lolium perenne*) is dominant with rough bluegrass (*Poa trivialis*) often co-dominant. In the parcels, that have been taken out of production longest Yorkshire fog grass (*Holcus lanatus*) Vernal grass (*Anthoxantum odoratum*) and sour dock (*Rumex acetosa*) are becoming more abundant. Clover species constitute less than 1% of the vegetation.

The second site, Oukoop, 4 km to the North East, was situated on an intensive dairy farm. The mast here has a free fetch area of at least 600 m in all directions. The management regime around the mast consisted of a mosaic of grass mowing and intensive rotational grazing during the period mid-May to mid-September (with each parcel of land receiving three cuts and 2–3 periods of grazing). Manure and fertilizer

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were applied two or three times a year, but not in winter. Average C and N content in the top 20 cm of the soils is 24% and 2.4%, respectively. Rye grass (*Lolium perenne*) is the most dominant grass species with rough bluegrass (*Poa trivialis*) often co-dominant. Clover species constitute less than 1% of the vegetation.

## 5 2.2 Meteorological instruments

Wind speed, air temperature and water vapour pressure were measured with an eddy covariance system consisting of a Campbell Csat C3 Sonic anemometer (Campbell Scientific, Logan, Utah, USA) directed into the main wind direction and a Licor 7500 open path Infrared gas analyser (LI-COR Lincoln, NE, USA). The gas analyser was calibrated, when necessary, with a calibration gas of known CO<sub>2</sub> concentration (between 370 and 400 ppm) and with air using a known H<sub>2</sub>O vapour concentration generated with a LI 610 dew point generator (LICOR) and with pure analytical grade Nitrogen. The gas analyser was checked for drift regularly (at least once a month) but was when re-calibrated, never found to have drifted more than 1% from the previous calibration.

15 Data were logged with a data logger (CR5000, Campbell Scientific). The mast was also equipped with micrometeorological sensors to measure short and long wave radiation (CRN1 Kipp and zonen, Delft, the Netherlands), photosynthetic photon flux density (Parlite, Kipp and zonen), air temperature and humidity (HMP 45a, Vaisala, Uppsala, Sweden) and air pressure (Druck CS115, Campbell Scientific). Soil measurement sensors included soil heat flux plates (HPF01) (Campbell Scientific n=6) and soil temperature sensors at depths of 2, 4, 8, 16, and 32 cm (Campbell Scientific) and soil moisture probes by volume (Theta probes ML 2x; Delta T devices Burwell UK). Rain was measured with a tipping bucket (0.1 mm) rain gauge (Young, Traverse City Michigan, USA). Water level was measured with a diver with pressure transducers (Ei-  
25 jkelkamp, Giesbeek, The Netherlands).

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## 2.3 Data analysis

Eddy covariance measurements were taken with a frequency of 10 Hz and integrated, as half hourly means with the EDDYFLUX software (O. Kolle MPI-BGC Jena following Carbo-Europe protocols: Aubinet et al., 2000). Data were filtered for spikes. Mean air pressure for each measurement period was used to correct fluxes for air density effects (Webb et al., 1980). Other corrections included linear detrending, and rotation to the local streamline (Baldocchi et al., 1988). Footprint estimates were calculated according to Schuepp et al. (1990). Quality control criteria according to Foken and Wichura (1996) were used to reject bad data. In addition we also filtered the data set for bad quality data due to temporary frost and dew, or moisture formation on the open path gas analyzer sensor head. This resulted in rejection of up to 50% of data during winter and up to 30% in summer for poor quality. From the remaining data set, storage fluxes were calculated from the CO<sub>2</sub> measurements at 3.05 m at the top of the mast according to Hollinger et al. (1994).

## 2.4 Gap filling

In order to provide estimates for the balance of net ecosystem exchange (NEE) we used a dual modelling approach for day and night time data to fill missing data gaps (Falge et al., 2001). For daytime data we used a Michaelis-Menten equation, which describes the functional relationship between Photosynthetic photon flux density (PPFD) and Ecosystem flux.

$$F_c = \frac{\alpha \times \text{PPFD} \times \beta}{\alpha \times \text{PPFD} + \beta} + \chi \quad (1)$$

Here  $\chi$  represents the ecosystem dark respiration,  $\alpha$  the ecosystem apparent quantum yield, and  $\beta$  the maximum downward ecosystem flux. As the sign of this flux is negative, it is further referred to minimum ecosystem flux.

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Missing data for ecosystem respiration were calculated using the Lloyd-Taylor equation.

$$R = R_{10} e^{E_0(1/(283.15-T_0)-1/(T-T_0))} \quad (2)$$

(a modified Arrhenius equation in which  $E_0=308.56$  K and  $T_0=227.13$  K). This empirical relationship allows for the calculation  $R_{10}$ , which denotes the ecosystem respiration at  $10^\circ\text{C}$  (Lloyd and Taylor, 1994).

Constants in Eq. (1) were fitted with non-linear regression (SPSS Statistical Package 12.1). Constants were fitted on a monthly basis or more often, when rapid changes in climatic conditions (once during a rapid temperature increase at the onset of spring in March 2005), or management interventions (grazing and mowing and rapid re-growth of the grass canopy thereafter) caused a change in the daily fluxes during that period. These periods were deduced from both flux measurements directly and the collected management data. Parameters were fitted for appropriate periods of between 7 and 14 days. For the estimate for  $R_{10}$  in Eq. (2) the total data set from each site was used.

## 2.5 Vegetation measurements and management data

Grass biomass and Leaf Area Index (LAI) were determined with a disc pasture meter (Eijkelkamp, Giesbeek, The Netherlands; plate weight 480 g, diameter 50 cm) by relating disc pasture meter height readings through linear regression to biomass in clipped samples (Bransby and Tainton, 1977). Grassland dry biomass ( $B_g$  in  $\text{g m}^{-2}$ ) was found to form a linear relationship with height ( $h$  in cm) following the equation  $B_g=29.1 \times h-50.2$  ( $R^2=0.84$   $n=51$ ;  $p<0.0001$ ) for a range of height measurements spanning 4 cm immediately after mowing to 35 cm in mature hay fields). Biomass removal was, when assessed with the disc pasture meter, taken as the difference between the height measurements taken before and after the event. Leaf area was determined by scanning subsamples from the harvested biomass and analyzing the scans with image analysis software (Image Pro Plus). Biomass samples were also separated in life and moribund biomass to correct LAI for life biomass proportion in maturing hayfields. Disc pasture

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height Measurements were made with 4–8 weekly intervals depending on the season. On each occasion, at least 20 measurements were taken per parcel of land within the fetch of the mast, resulting in the order of 200 measurements per site. For comparison of LAI with the eddy covariance data were kept for all fields that were contributing to the tower footprint in a radius of approximately 500 m. Biomass removal by the farmer was assessed by taking the mean vegetation height before and after the mowing of the vegetation. For grazing periods in a field (the farmer uses short rotation intensive grazing periods of 2–3 weeks or shorter) we compared grass height increments in adjacent fields with the height in the grazed fields.

Independently from our records, and without communication about intermediate results, the farmer also kept records of biomass removal estimates from each field (Range 1–3.5 tones dry matter ha<sup>-1</sup> with a resolution of approximately 0.2 tones dry matter ha<sup>-1</sup>). The farmer also kept detailed records of short rotation grazing periods (exact dates) and manure gifts (data in m<sup>-3</sup> ha<sup>-1</sup>). We were unable to independently accurately quantify manure gift data, but farmers in the Netherlands are by law required to keep detailed records of manure gifts and these records are inspected by legal authority. The accuracy of grazing period records were cross-checked with our own field management observations. We did not observe instances, where the farmer had not recorded his management.

Finally, compiled data of biomass production were cross checked against production standards generally and independently established for this grassland and management type and manure regime in the Netherlands (Oenema et al., 2005).

## 2.6 Laboratory analyses

Well-stirred samples of the slurry manure were sampled just before the first manure application and analyzed for dry matter and C content gravimetrically.

Leaf samples of the grassland crops were taken at 4–8 week intervals for each of 5–8 parcels in the main footprint of the mast. Bulk samples consisted of 20 subsamples of 5–10 leaves sampled randomly from the grass canopy. N and P were analyzed

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with an auto-analyzer (Sanplus, Eastwood, Australia), after drying the leaf samples to constant weight at 80°C and acid digestion in sulphuric acid, Selenium and salicylic acid. Standard reference samples with known N & P content were included in each analysis run (Novozamsky et al., 1983).

## 3 Results

### 3.1 Climatic conditions

The measurement period stretched from the end of the farming season October 2004 to the end of the farming season September 2005. Monthly temperatures during this period were comparable to the average period but for January 2005, which was warmer than usual (Fig. 2). Precipitation was lower in the autumn and winter of 2004/05 while rainfall was higher than usual in July–September 2005. A short heat wave was experienced around 20 June 2005, when air temperatures reached maxima around 35°C. Maximum Vapor Pressure deficit ranged from maximally 1.5 kPa during warm periods in autumn and spring to <0.6 kPa during winter and early spring. During a short very warm period around 20 June VPD rose as high as 3.5 kPa.

Groundwater levels varied between 30 cm below the surface to 60 cm in June in Oukoop, where the farmer has installed a drainage system. As a result soil moisture conditions in the plant root zone (10–30 cm) were for most of the measurement period best characterized as wet in both sites with soil moisture values generally around 50% to 60% by volume. During the driest period in June soil moisture values did not drop below 25% in Oukoop and 31% in Stein (not shown).

### 3.2 Vegetation

Leaf nutrient concentrations of N and P were for most of the time in both sites similar with concentrations around 2500 mmol N kg<sup>-1</sup> dry weight and 150 mmol P kg<sup>-1</sup>

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respectively (Fig. 3a). In April (Julian day 105) concentrations of both nutrients were increased in Oukoop, possibly because of contamination of the plant material from a slurry manure gift on the farm some days earlier. In May/June leaf nutrient concentrations declined in both sites, but most strongly in Stein.

At the beginning of the measurement period, mean standing biomass was in both sites  $180 \text{ g dry weight m}^{-2}$  (Fig. 3b). Standing biomass declined steadily throughout winter due to shoot mortality and heavy grazing by Graylag geese and Widgeon. Biomass increased rapidly again, with the onset of spring after a cold spell in the second week of March (up to Julian day 72). Farming exploitation of the grass started in Oukoop with mowing of the vegetation on 12 May (Julian day 131). From then onwards parcels in Oukoop were mown two more times and grazed in a rotational scheme until the end of September. Individual parcels of land were mown, when vegetation height (as measured with the disc pasture meter) reached 20–22 cm. In Stein most parcels were used as hay land and mown at a height of on average 32 cm on 14 June (Julian day 165). A number of parcels were again mown around Julian day 210, whereas more distant parcels ( $>150 \text{ m}$  but still potentially in the footprint from the mast) were intermittently stocked with a small number ( $n=20$ ) of 1 year old dairy cattle until the end of August.

### 3.3 Energy balance measurements

Incoming solar radiation ranged between maximally  $300 \text{ W m}^{-2}$  in December and January to  $850 \text{ W m}^{-2}$  in June/July. Energy was dissipated in both sites more in latent ( $\lambda E$ ) than in sensible ( $H$ ) heat. This partitioning of energy is shown for Stein in the first half of June when maximum biomass was reached (Fig. 4). This pattern is typical of wetland ecosystems. Heat partitioning resulted in Bowen ratios ( $\beta$ ) below unity throughout the year. Only during the warm period around 20 June did  $\beta$  rise above unity briefly to maximally 1.5 in Stein. The extent to which measured  $\lambda E$  and  $H$  accounted for the available energy is shown for both sites for April (Fig. 5) when vegetation conditions were similar. Here ( $H+\lambda E$ ) are plotted against ( $R_n-G$ ),  $R_n$  being the net radiation and

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$G$  being the soil heat flux at 0.02 m depth. Both sites showed the same characteristics of energy balance closure. At night estimates of  $(H+\lambda E)$  were higher than  $(R_n-G)$ , with the eddy system apparently not measuring the night time heat flux. At low insolation in the early morning (not shown)  $(H+\lambda E)$  rose above values of  $(R_n-G)$  while by late afternoon a reverse trend was visible. At high insolation, estimates of  $(H+\lambda E)$  were up to 20% lower than estimates of  $(R_n-G)$  as is usually found in eddy covariance measurements, particularly in wetlands (Moncrieff et al., 1997; Kurbatova et al., 2002; Corradi et al., 2005; Nieveen et al., 2005).

### 3.4 Coupling with the atmosphere

$\text{CO}_2$  flux rate measurements may be reduced under conditions of low turbulence, due to  $\text{CO}_2$  storage and instrumental limitations. This was investigated by examining the effect of the friction velocity ( $u^*$ ) on the measured nighttime  $\text{CO}_2$  fluxes. In Fig. 6, the data set for July 2005, the month with the highest nighttime fluxes was compared for both sites. Measured fluxes were found to be reduced below  $0.1 \text{ m s}^{-1}$ , as typically observed in eddy covariance measurements over open grassland and savanna ecosystems (Nieveen et al., 2005; Veenendaal et al., 2004; Lloyd, 2006). Periods with  $u^*$  values lower than  $0.1 \text{ m s}^{-1}$  commonly occurred during quiet weather, particularly at night, for several hours. Correcting for the storage fluxes did not significantly alter the relationship between night time fluxes and  $u^*$  (not shown). Therefore, for calculations of the final fluxes, a filter was applied of  $u^* < 0.1 \text{ m s}^{-1}$  after first correcting for the storage flux.

### 3.5 Net ecosystem exchange

Footprint calculations (Schuepp et al., 1990) gave under turbulent conditions values of 25–30 m for foot peak, 70–90 m for 50% fetch and 500–600 m for 90% fetch distance. Net ecosystem exchange (NEE) varied in relation to changing seasonal climate conditions and management interventions. Figure 7 shows the relation between NEE and

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PPFD for the Stein site and Oukoop site in January and April. Seasonal variation in parameter values are given in Table 1.

There was no apparent seasonal trend (not shown) in calculated ecosystem respiration at 10°C ( $R_{10}$ ; necessary for Eq. 2;) and  $R_{10}$  was subsequently derived from the whole data set of night time fluxes at each site. The dataset for Stein is shown in Fig. 8.  $R_{10}$  was 3.47  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  for Stein (95% confidence interval 3.33 to 3.62  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ). The  $R_{10}$  for Oukoop was marginally higher at 3.64  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  (95% confidence interval 3.49 to 3.80  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ).

### 3.6 LAI, temperature, minimum ecosystem flux and apparent quantum yield

Minimum ecosystem flux ( $\beta$ ) naturally showed a strong correlation with LAI (Table 1), except in Stein in May and June when minimum ecosystem flux ( $\beta$ ) did increase further at higher LAI (>8). In this period the grasslands in the footprint of the Stein tower developed into mature hayfields (LAI>8) and leaf nutrient concentrations dropped. Disregarding mature hay land data points in the analysis, linear regression of LAI against  $\beta$  did show significant differences between Oukoop and Stein (Fig. 9; regression equation of the combined data set:  $\beta = 17.95 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} - 11.22 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} \times \text{LAI}$ . ( $P < 0.001 R^2 = 0.87 n = 22$ ).

LAI also strongly correlated with mean daily temperature (not shown) and both LAI and temperature co-varied. When only considering data from the growing season (main growing season mid March to late October; mean daily temperature range 9.9°C–17.6°C), there was no significant correlation between  $\beta$  and temperature ( $R^2 = 0.03 n = 13$ ), but still a very strong correlation with LAI ( $P < 0.005 R^2 = 0.55 n = 13$ ). Thus LAI was during the growing season the main driver for  $\beta$ .

Ecosystem apparent quantum yield ( $\alpha$ ) was variable and not significantly different between the two sites, although there was a non-significant trend for  $\alpha$  to be smaller with low LAI and temperature. When only considering data from the main growth season,  $\alpha$  was not significantly related to temperature, but there was a significant relationship

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with LAI ( $P > 0.05$  ( $R^2 = 0.40$   $n = 13$ ; regression equation  $\alpha = -0.018 \mu\text{mol CO}_2 \mu\text{mol}^{-1}$  photons  $\times$  LAI  $+ 0.20 \mu\text{mol CO}_2 \mu\text{mol}^{-1}$  photons). Mean value for  $\alpha$  for the whole data set was  $-0.45 \mu\text{mol CO}_2 \mu\text{mol}^{-1}$  photons (95% conf. Limits mean.  $-0.38$  to  $-0.52 \mu\text{mol CO}_2 \mu\text{mol}^{-1}$ ).

### 5 3.7 Partitioning of seasonal and annual CO<sub>2</sub> fluxes

From October 2004 onwards, when measurements began, both sites were a source of CO<sub>2</sub> (Fig. 10a) emitting  $50\text{--}100 \text{mmol m}^{-2} \text{d}^{-1}$  on average, reducing to close to  $10 \text{mmol m}^{-2} \text{d}^{-1}$  during cold frost periods with low biomass. Early March (Julian day 70) when the cold period ended and daily irradiance increased, NEE rapidly became negative, reaching uptake values below  $-400 \text{mmol m}^{-2} \text{d}^{-1}$ . The first mowing of the parcels turned the Oukoop site temporarily into a source of CO<sub>2</sub> (mid May, Julian day 134). Similarly, Stein became a source, when nearly all parcels of land in the footprint of the mast were mown on 14 June (Julian Day 165). Further variation in the NEE was until mid September in both sites caused by grazing and/or mowing of parcels of land in the footprint area, particularly in the Oukoop farm.

Ecosystem respiration  $R$  (Fig. 10b; measured at night; calculated from Eq. (2) during the day) was higher in Oukoop during the winter period. Lowest daily values were  $50 \text{mmol CO}_2 \text{m}^{-2} \text{d}^{-1}$ . These were observed found in both sites at a soil temperature (0.02 m) of  $0^\circ\text{C}$ .  $R$  reached its peak in mid July at around  $600 \text{mmol CO}_2 \text{m}^{-2} \text{d}^{-1}$  in Stein and around  $800 \text{mmol CO}_2 \text{m}^{-2} \text{d}^{-1}$  in Oukoop when soil temperatures rose to  $20^\circ\text{C}$  around Julian day 190.

Gross ecosystem photosynthesis (GEP, Fig. 10c) was calculated by subtracting  $R$  from NEE. Throughout the year the grass canopy was green and able to photosynthesize with lowest values of near  $0 \text{mmol CO}_2 \text{m}^{-2} \text{d}^{-1}$  during cold frost periods, especially with low insolation. Minimum values for GEP around  $-800 \text{mmol CO}_2 \text{m}^{-2} \text{d}^{-1}$  were observed by the beginning of May, coinciding with LAI estimates near 6. Further increases in LAI in the stein site did not result in a further decrease in GEP suggesting

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that  $-800 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$  is about the minimum value, that can be reached by this vegetation type.

### 3.8 Annual NEE, GEP and R balances

The resulting annual NEE balance showed for the measurement period a divergence with Oukoop exchanging up to  $2.9 \text{ mol CO}_2 \text{ m}^{-2}$  more to the atmosphere in the winter months than the Stein site, mainly as a result of a higher respiration (Fig. 11 estimated cumulative difference for  $R$  was  $3.5 \text{ mol a}^{-1}$ ). Large differences in cumulative NEE developed with grazing and mowing of the Oukoop site from Early May on. Oukoop then became a net source for  $\text{CO}_2$ . Similarly the Stein site temporarily became also a source for  $\text{CO}_2$  after mowing in June. For the whole period the annual cumulative NEE for Stein was  $-0.7 \text{ mol CO}_2 \text{ m}^{-2} \text{ a}^{-1}$  and for Oukoop  $+10.2 \text{ mol CO}_2 \text{ m}^{-2} \text{ a}^{-1}$ . The annual balance could be partitioned in an annual  $R$  estimate of  $126.7 \text{ mol m}^{-2} \text{ a}^{-1}$  and a GEP of  $-127.4 \text{ mol CO}_2 \text{ m}^{-2} \text{ a}^{-1}$  in Stein. These figures show  $129.1 \text{ mol CO}_2 \text{ m}^{-2} \text{ a}^{-1}$  and  $-118.8 \text{ mol CO}_2 \text{ m}^{-2} \text{ a}^{-1}$  for  $R$  and GEP, respectively, in Oukoop.

### 3.9 Biomass removal by cutting and grazing

For the Stein site the total amount of above ground biomass removed in June was estimated at  $6.3 \text{ tonnes dry matter ha}^{-1}$ , averaged for the fetch area of the mast, based on disk pasture measurements. For individual fields this figure ranged between 0 and  $7.2 \text{ tonnes dry matter ha}^{-1}$  as all but one field were in the first instance mown on the same day, the 15 June 2005 (mean height of parcels of land was before mowing 29–35 cm and 6–8 cm immediately after mowing). One field was mown in July and some fields were grazed in July and August, which resulted in an additional area averaged removal of  $3.0 \text{ tonnes dry matter ha}^{-1}$  up to August (estimated range 2–4 tonnes dry matter  $\text{ha}^{-1}$ ). Total biomass removed thus amounted to  $9.3 \text{ tonnes dry matter ha}^{-1} \text{ a}^{-1}$  or  $470 \text{ g C m}^{-2}$  ( $39 \text{ mol C m}^{-2}$ ; average C content of removed dry matter =50%; range 7–11 tonnes dry matter  $\text{ha}^{-1}$ ). During a six week period in July/August young cattle

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were permanently grazing in three parcels of land, which potentially contribute to the footprint. Their respiration contribution would be included in the Eddy measurements. Live weight gains in the period would have been small (see e.g. Lloyd, 2006). The standing biomass at Stein reduced by at least another 1 ton dry matter ha<sup>-1</sup> during the winter months, partly through grazing by water fowl. As these stay mostly in the fields, winter C export from the ecosystem (other than measured by EC) was considered negligible.

In Oukoop biomass removal data based on the farm record amounted to 6.5 tonnes dry matter ha<sup>-1</sup>. Disc pasture meter measurements generally gave on average up to 20% lower estimates. Grazing removed 2.5 tones dry matter ha<sup>-1</sup> (estimated range 2–3 tonnes kg dry matter ha<sup>-1</sup>) putting total dry matter biomass removal at 9.0 tonnes dry matter ha<sup>-1</sup> a<sup>-1</sup> (range estimate 8–10 tonnes dry matter ha<sup>-1</sup>) or 450 g C m<sup>-2</sup> a<sup>-1</sup> (36 mol C m<sup>-2</sup> a<sup>-1</sup>). Slurry manure gifts amounted to a total area averaged gift of 57.8 m<sup>3</sup> ha<sup>-1</sup> a<sup>-1</sup> (given over 4 gifts ranging from 28 m<sup>3</sup> ha<sup>-1</sup> in February 2005 in all fields to 13 m<sup>3</sup> ha<sup>-1</sup> on a field in September; farmer's record). On the basis of a C content of 26.4±1.8 g C kg<sup>-1</sup> slurry manure (mean ±1 s.e.) and a specific weight of the slurry manure of 1.08±0.01 kg kg<sup>-1</sup> (Determined from the first slurry gift) the annual remittal of C through manure into the field was estimated at 142 g C m<sup>-2</sup> a<sup>-1</sup> (11.8 mol C m<sup>-2</sup> a<sup>-1</sup>; range 122–151 g C m<sup>-2</sup> a<sup>-1</sup>; error due to mistake in farm record not included).

## 4 Discussion

### 4.1 Uncertainties in EC measurements

Eddy covariance data carry an uncertainty that should be considered carefully as measurements are not replicated within site (Moncrieff et al., 1996). For instance Baldocchi et al. (2001) estimate an average uncertainty of 4 mol C m<sup>-2</sup> a<sup>-1</sup> for closed-path eddy covariance systems, while Hendriks et al report an error in the measurements of 13% or 3 mol C m<sup>-2</sup> a<sup>-1</sup> for an open path system with similar data loss as in this study. Our

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sites were also equipped with open-path EC systems, that showed an energy balance closure similar to other comparable systems (Hsieh et al., 2005; Kurbatova et al., 2002; Moncrieff et al., 1997; Nieveen et al., 2005) even though energy balance closure is difficult in wetland areas due to poor, or lacking estimates of soil and water energy fluxes (Corradi et al., 2005). In our site during late afternoon under lower insolation, the eddy system gives a higher estimate of the latent and sensible heat flux, than the radiation and soil heat flux (not shown), suggesting that some of the energy is stored (e.g. in the water ditches), where it is not measured by the instrumental setup.

Poor turbulence, rain and/or mist led to a significant proportion (in winter up to 50%) of the raw data to be discarded. At the same time parameterization of data may then be difficult because of low fluxes. Regression errors multiply with gap filling, and can exaggerate site differences during prolonged periods of data loss (Falge et al., 2001; Reichstein et al., 2005). Most difficult may be the parameterisation, when the management around the footprint of the mast is not homogeneous, as was the case in Oukoop due to agricultural management in spring and summer. However, the observed strong relationship between  $\beta$  (modeled minimum ecosystem flux) and LAI gives an insight into the replicability of the results and indicates that this will not have had a major effect on the measurement error normally reported for EC systems. With similar LAI and Leaf nutrient levels present similar variation was measured in NEE. During the period of highest NEE and  $R$  in spring and summer the need for gap filling is at any rate much smaller due to more favorable weather conditions.

## 4.2 Fluxes and management

The biomass and LAI measurements can be used to compare our sites with other grasslands and to check consistency of the measured flux components. However the uncertainty in the management data itself also needs to be explored in detail, as they present a significant proportion of the carbon budget and the management particularly in Oukoop in the tower fetch area is partially inhomogeneous.

The measured range of LAI of 2 to 5 and for hay lands >8 for a biomass range of 1.5

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to 7 tonnes ha<sup>-1</sup> dry matter in our sites is consistent with LAI measurements for other rye grass swards (see e.g. Lamb et al., 2002).

Also the production estimates are within the expected range. Long term yield trials (the “van Steenberghe” trials) in the Netherlands predict a yield of 9 to 10 tonnes dry matter ha<sup>-1</sup> on an unfertilised grasslands on peat soil with a range of 1.5 tonnes ha<sup>-1</sup> (Schothorst, 1977; Oenema et al., 2005). The biomass removal estimate for Stein falls within this predicted range and is thus confirmed by independent data. In Stein management was homogeneous up to and also largely after the first biomass removal on 15 June and could therefore be monitored in detail.

A rye grass sward with high manure and fertiliser input, as in Oukoop can potentially produce up to 14 tonnes dry matter ha<sup>-1</sup>, which is considerably more than our measured value (Oenema et al., 2005). However, the high mowing and grazing frequency applied at Oukoop (which increases grazing quality and effective milk production) reduces maximum biomass production. Experimental farm trials (see e.g. Korte and Harris, 1987) suggest that with 3 to 4 mowing events a 20–30% reduction must be expected. Our disc pasture measurements give a lower figure than the farmer’s biomass removal records, but this in this site there is generally a greater time delay between our last height measurement, the moment the farmer decided to mow the herbage and our height measurements thereafter. We therefore took the farmer’s own record to be the more precise one. A detailed production assessment in nearby farm with comparable management in Oenema et al. (2005) gave over the period 2000–2003 a mean production figure of 10.1 tonnes ha<sup>-1</sup> a<sup>-1</sup> (range 9.2–11.1 tonnes ha<sup>-1</sup> a<sup>-1</sup>). This suggests that our annual estimate for Oukoop at 9 tonnes ha<sup>-1</sup> a<sup>-1</sup> is on the low side of the spectrum. EC measurements, which put GEP somewhat lower in Oukoop compared to Stein (difference 8.5 mol C a<sup>-1</sup> or 9%) appear to support the Oukoop biomass estimate, although differences in biomass removal regime may lead to changes in root shoot allocation in the sward.

The estimates for ecosystem respiration at 10°C, ( $R_{10}$ ) of 3.47 and 3.64 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> are within the range reported for other temperate eutrophic fen meadows,

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agricultural systems and higher parts of temperate bogs (range 2.3–3.9; Anthoni et al., 2004; Hsieh et al., 2005; Nieveen et al., 2005; Lafleur et al., 2005; Lohila et al., 2003).

Site and seasonal differences in  $R_{10}$  may be due to the amount of digestible dead matter for heterotrophic respiration, but also to the living biomass (autotrophic respiration) present during the measurement period. For the latter, Lloyd (2006) recently estimated a contribution to  $R$  from standing biomass of 6–7% considering the high mowing frequency in spring and summer. This could lead to a somewhat reduced cumulative  $R$  in Oukoop compared to Stein. Lloyd (2006) also showed a significant effect from the groundwater table, which varied strongly in his study, but was less variable in our study. In Oukoop  $R$  may also be influenced by the annual slurry application (in the order of  $142 \text{ g C m}^{-2} \text{ a}^{-1}$ ), most of which is supposedly respired rapidly (Anthoni et al., 2004; Vuichard et al., 2007).

NEE was strongly influenced by the vegetation. For instance, the mean apparent quantum yield ( $\alpha$ ) in our site amounted to  $0.45 \mu\text{mol CO}_2 \mu\text{mol}^{-1}$  photons and is similar to that reported for closed canopy grasslands (Ruimy et al., 1995). Lower values, reported by for instance Nieveen et al., (1998, 2005), may be associated with low NEE and therefore likely also low LAI. Half hourly maxima of NEE were around  $-30 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  and linearly related with LAI except during the maturation phase of the grass canopy. Minimum NEE may be influenced by dry weather conditions resulting in a high vapour pressure deficit (VPD; Hunt et al., 2002; Arneth et al., 2006). However, for temperate grasslands on peat, VPD effects are not well documented. The reduction in NEE reported by Nieveen et al. (2005) due to reduced soil moisture and a VPD of 1.6 kPa was not separated from variation in LAI. In our study the only time when VPD was for a short period greater than 1.5 kPa (June 2005) coincided with mowing and grazing of both sites and a reduced LAI. The summer months July and August were in 2005 wetter than usual and the effect could not be studied further. Higher VPD's are in our study area not very common anyway (Dirks et al., 1999), but may become so with future warming trends.

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### 4.3 Carbon balance

The difference in NEE between the two sites of  $-131 \text{ g C m}^{-2} \text{ a}^{-1}$  with higher uptake from the atmosphere in Stein appear less driven by ecosystem respiration (annual difference  $30 \text{ g C m}^{-2}$ ; higher in Oukoop) than by GEP (annual difference  $-101 \text{ g m}^{-2}$ ) and results in a marginal sink estimate of  $-8.4 \text{ g C m}^{-2} \text{ a}^{-1}$  in Stein and a source estimate of  $122.4 \text{ g C a}^{-1}$  in Oukoop. However, for a complete C balance, also biomass off take, slurry input and Non-CO<sub>2</sub> trace gas emissions, in particular methane, have to be included.

In Stein biomass removal during the measurement period was  $470 \text{ g C m}^{-2} \text{ a}^{-1}$  probable range (estimated range  $420\text{--}530 \text{ g C m}^{-2} \text{ a}^{-1}$ ). Methane emissions from the area are at present uncertain. However, no manure is applied in the area, cattle are virtually absent and water level is 30 to 50 below the surface. Therefore, C losses through methane in the field are relatively small (Van den Pol-Van Dasselaar et al., 1999a, b; Hensen et al., 2006). The estimated C balance of the Stein location would then be a loss of  $462 \text{ g C m}^{-2} \text{ a}^{-1}$  with similar range as before.

In Oukoop the balance is more difficult to estimate due to the mosaic of mowing, grazing and cow slurry manure gifts that are brought back into the field. The biomass removal through mowing and grazing was in this year estimated at  $450 \text{ g C m}^{-2} \text{ a}^{-1}$  (estimated range of  $400\text{--}500 \text{ g C m}^{-2} \text{ a}^{-1}$ ). Manure gifts amounted to  $142 \text{ g C m}^{-2} \text{ a}^{-1}$  input back into the soil. However, there is more manure directly deposited by cattle in the field. The latter we estimate at about 10% or  $14 \text{ g C m}^{-2} \text{ a}^{-1}$  of the slurry application (on the basis of assumed continuous digestion and that cattle spent ca.  $6 \text{ h d}^{-1}$  in the field between June and September). Respiration losses from cows in the field are doubly measured (grass consumed is a loss and cattle respired CO<sub>2</sub> in the footprint is measured), but assumed negligible (cattle spend an estimated <2% of their time annually in the direct footprint of the mast). Methane losses from soil in our drained peat ecosystem are again considered negligible in terms of C balance. Methane losses from manure, cattle and slurry tanks could be significant. Applying emission data for Dutch

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dairy farms of up to  $95 \text{ kg CH}_4 \text{ d}^{-1}$  (maximum for large farms; Hensen et al., 2006) and assuming half of the cattle feed emanating from outside the Oukoop farm, this results for our farm (50 ha) in an estimate of  $35 \text{ g C m}^{-2} \text{ a}^{-1}$  or 10% from the field produced C emitted in the form of methane through cattle. Per head estimates (Vuichard et al., 2007) would result in a similar figure for Oukoop. This is of less consequence for the C balance, but the more so for the greenhouse gas balance. We are presently quantifying the estimates for methane emissions with actual measurements. However, taking methane emissions into account, the balance of C from the Oukoop site is then estimated to be  $465 \text{ g m}^{-2} \text{ a}^{-1}$ . The uncertainty of this figure is larger than in Stein, not only because the biomass removal estimate is on the low side of the expected range but also uncertainty remains in particular with regard to the precise figure of manure and the greater uncertainty of methane emissions. However the estimate indicates that both sites are more similar in carbon balance than NEE measurements alone would suggest and sources of a similar magnitude

C losses from Stein and Oukoop are thus in the order of  $462 \text{ g C m}^{-2} \text{ a}^{-1}$  and  $465 \text{ g C m}^{-2} \text{ a}^{-1}$  and of similar magnitude. They are also 3 to 4 times higher than previously reported for eutrophic fen meadow ecosystems in New Zealand, United Kingdom or for the Netherlands (Langeveld et al., 1997; Nieveen et al., 2005; Lloyd, 2006). They are, however, consistent with and in the same order of magnitude as estimates based on peat oxidation and subsidence (Schothorst, 1977). They contrast sharply with recent results from a 14 year old fen restoration project on a former fen meadow (Hendriks et al., 2007) which has a sink strength of  $262 \text{ g m}^{-2} \text{ a}^{-1}$ .

## 5 Conclusion

Different management regimes in the result in differences in NEE and its partitioning, which is directly influenced by management interventions (mowing, grazing, and manuring). When estimating the net C balance, both sites are strong sources for C of comparable magnitude largely due to similar biomass removal.

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**Table 1.** Seasonal variation in Leaf Area index (LAI m<sup>2</sup> leaf m<sup>-2</sup> ground), mean daily temperature (°C) and monthly fitted parameters for apparent quantum yield ( $\alpha$ ;  $\mu\text{mol CO}_2\mu\text{mol}^{-1}$  photons), minimum ecosystem flux ( $\beta$ ;  $\mu\text{mol CO}_2\text{ m}^{-2}\text{ s}^{-1}$ ) and dark respiration ( $\chi$ ;  $\mu\text{mol CO}_2\text{ m}^{-2}\text{ s}^{-1}$ ). Parameters fitted with daytime flux data in Eq. (1). (Numbers in brackets denote 1 s.e.; \* calculated from a Different period for Oukoop, therefore different mean daily temperature).

Period	Oct	Nov	Dec	Jan	Feb	March	April	May	June	July	Aug	Sep
Mean temp Stein/Oukoop	11.2	6.3	3.2	5.1	2.3	10.4	9.9	12.2/10.6*	12.9/16.4*	17.4	16.1	15.3/13.6*
Stein												
Mean LAI	3	2.6	2.3	2.1	2	3.1	4.2	8	8	3.7	3.7	3.6
$\alpha$	-0.040	-0.042	-0.019	-0.046	-0.038	-0.031	-0.050	-0.041	-0.040	-0.046	-0.056	-0.036 (0.009)
(s.e.)	(0.006)	(0.017)	(0.079)	(0.024)	(0.028)	(0.007)	(0.005)	(0.003)	(0.007)	(0.005)	(0.009)	
$\beta$	-15.3	-12.2	-1.2	-7.5	-6.6	-20.5	-27.3	-33.6	-28.4	-24.3	-22.1	-15.9
(s.e.)	(1.0)	(3.2)	(1.3)	(1.5)	(1.4)	(2.6)	(1.1)	(2.1)	(1.1)	(1.0)	(0.9)	(1.3)
$\chi$	3.8 (0.4)	2.5 (0.7)	-0.10	1.9 (0.7)	1.8 (0.9)	2.9 (0.6)	3.9 (0.6)	6.0 (0.3)	7.1 (0.8)	7.1 (0.5)	7.0 (0.7)	4.2 (0.7)
(s.e.)			(1.0)									
Oukoop												
Mean LAI	3.2	2.8	2.6	2.3	2	3.1	4.1	3.5	4.2	3.5	3.9	no value
$\alpha$	-0.027	-0.060	-0.027	-0.078	no	-0.031	-0.048	-0.065	-0.058	-0.052	-0.058	-0.055
(s.e.)	(0.008)	(0.018)	(0.022)	(0.067)		(0.005)	(0.004)	(0.013)	(0.008)	(0.006)	(0.008)	(0.023)
$\beta$	-14.0	-12.8	-10.5	-5.4	values	-22.5	-32.7	-27.0	-26.9	-21.2	-26.6	-15.8
(s.e.)	(1.0)	(3.2)	(1.3)	(1.5)		(2.6)	(1.1)	(1.1)	(2.1)	(1.0)	(0.9)	(1.3)
$\chi$	2.0	3.1	1.9	2.6		3.3	4.0	6.3	8.5	7.5	7.6	4.1
(s.e.)	(0.6)	(0.6)	(0.9)	(1.0)		(0.5)	(0.5)	(1.0)	(0.7)	(0.5)	(0.6)	(1.3)

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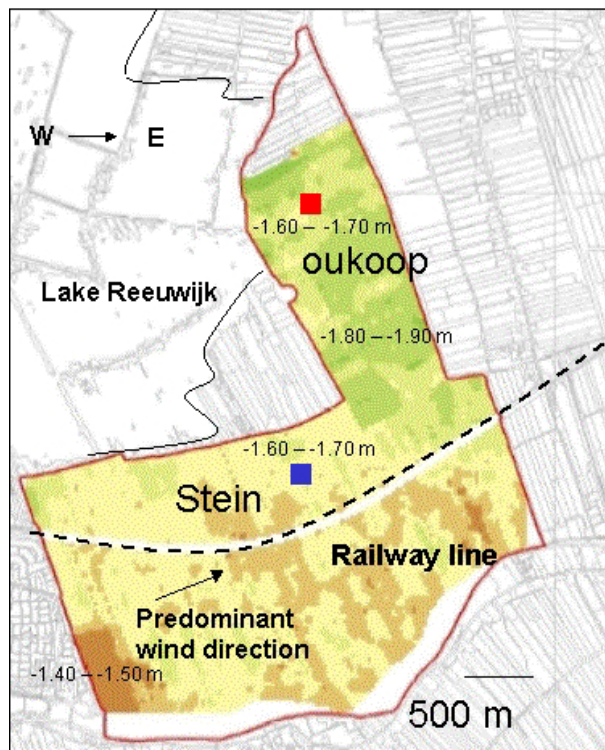
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**Fig. 1.** Map of the research site at Reeuwijk. (Colours indicate mean elevation below sea level as indicated in the figure; blue square: Location micro-meteorological tower in Stein ( $52^{\circ}, 01', 7.35''$  N;  $4^{\circ}, 46' 43.45''$  S), red square: Oukoop ( $52^{\circ}, 02', 10.98''$  N;  $4^{\circ}, 46' 49.55''$  S)).

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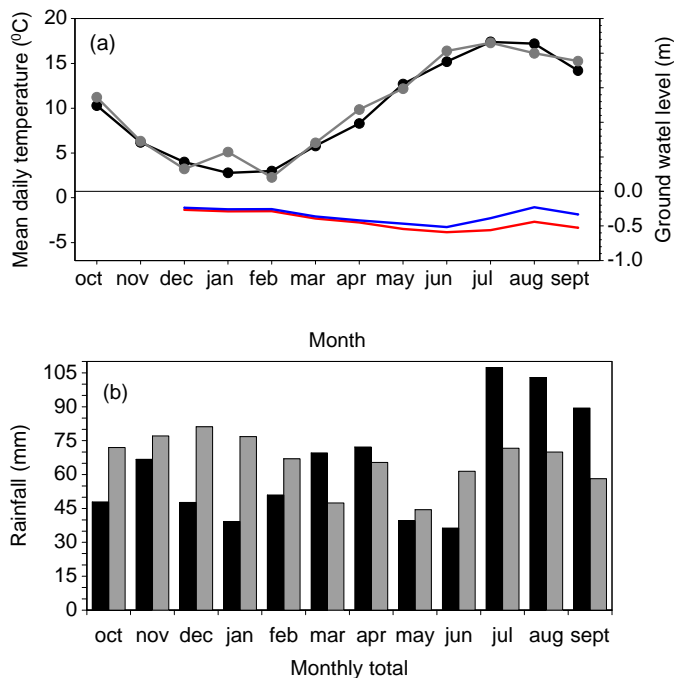
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**Fig. 2. (a)** Monthly (grey circles: Stein) and 30 year average (black circles: period 1975–2005), temperature and ground water level (blue line: Stein; red line: Oukoop; period December 2004–September 2005). **(b)** Rainfall (black bars: October 2004 to September 2005; grey bars: 30 year average; period 1975 to 2005).

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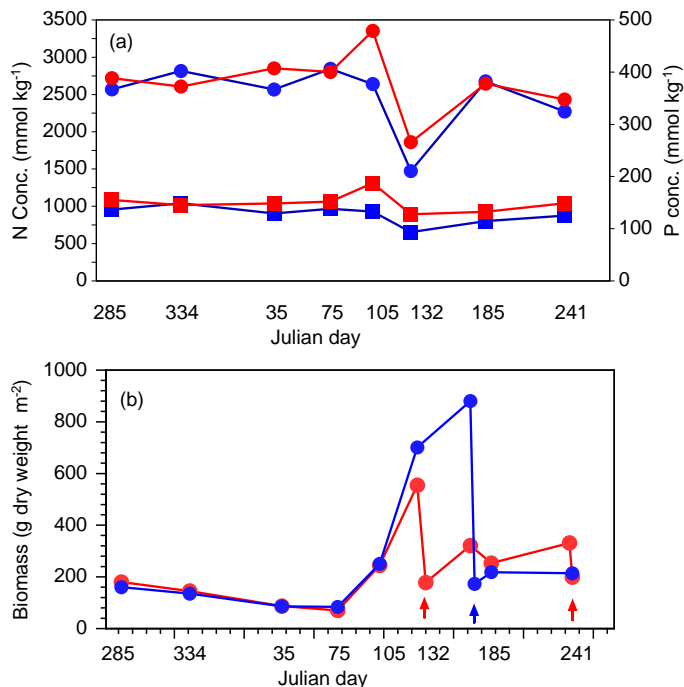
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**Fig. 3. (a)** Leaf concentrations of Nitrogen (N: blue circles: Stein; red circles: Oukoop) and Phosphorus (P: blue squares: Stein; red squares: Oukoop). Period: October 2004 to September 2005, Julian day indicates day of sampling. **(b)** Standing biomass (blue circles: Stein; red circles: Oukoop). Period: October 2004 to September 2005. Arrows indicate main mowing events.

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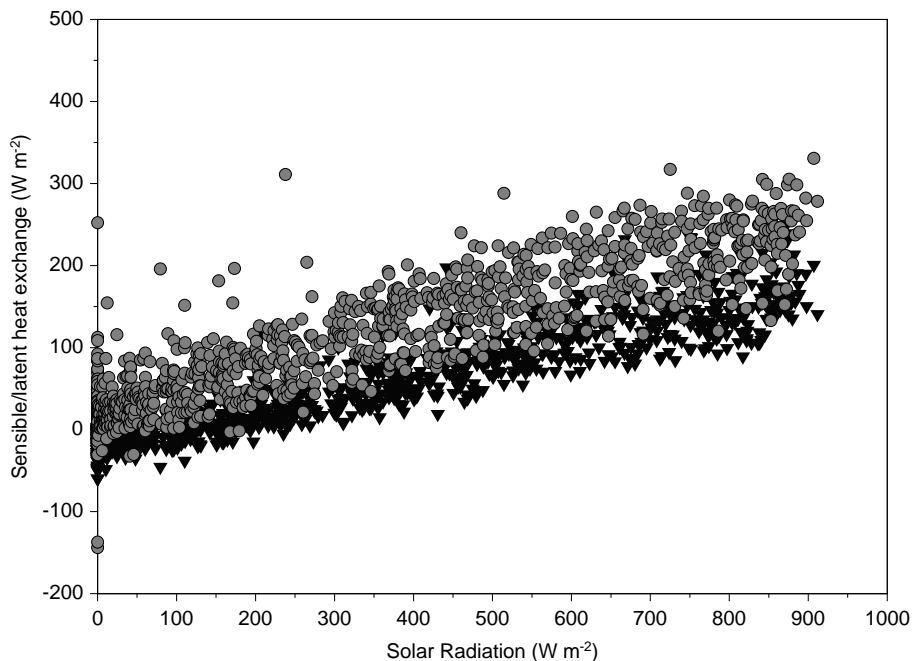
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**Fig. 4.** Latent and sensible heat flux in response to solar (or shortwave downward) radiation (black triangles: Sensible heat exchange; grey circles: Latent heat exchange). Data for Stein from June 2005 at maximum vegetation biomass, before mowing.

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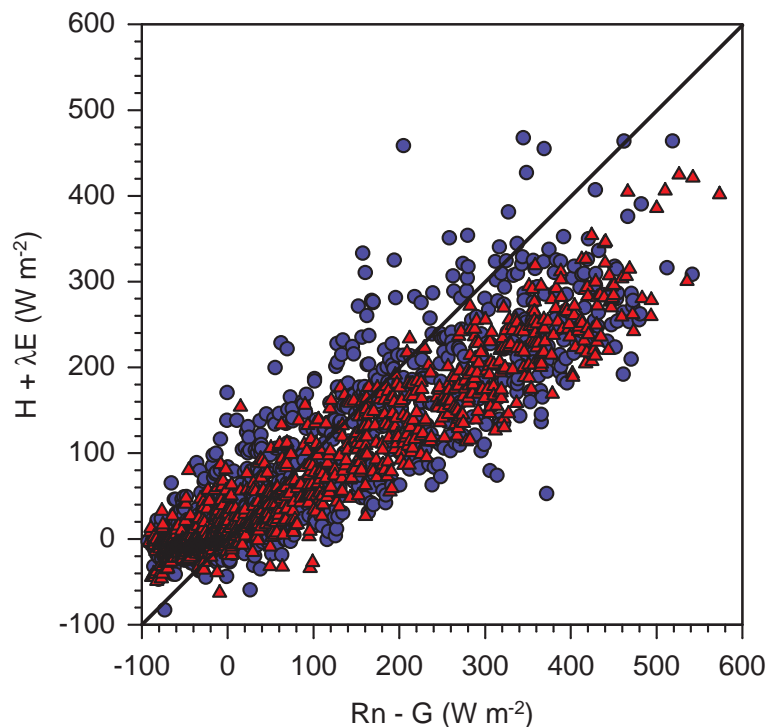
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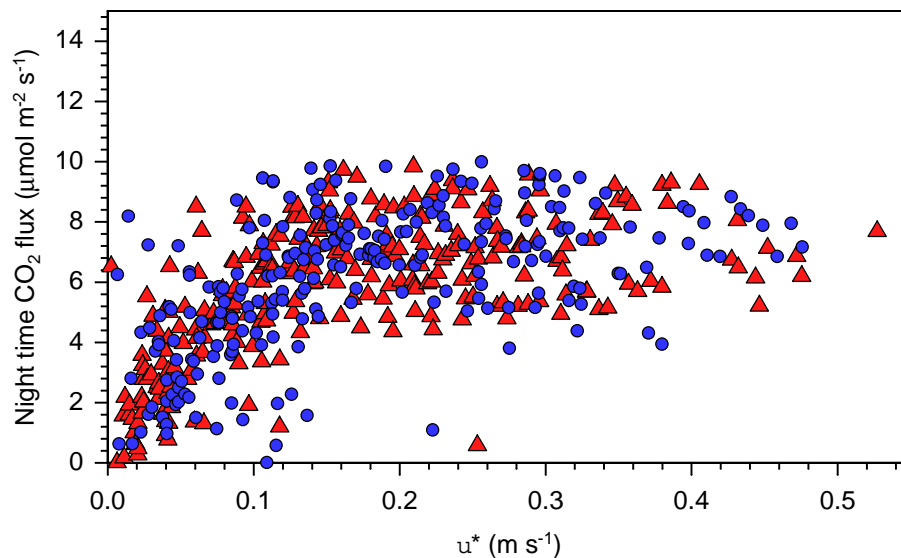


**Fig. 5.** Comparison of the energy balance closure of eddy covariance measurements of Sensible ( $H$ ) and latent ( $\lambda E$ ) heat exchange and radiation measurements: net radiation ( $R_n$ ) – soil heat flux ( $G$ ). The solid line indicates  $x=y$ . (blue circles: Stein; red triangles: Oukoop; measurements taken in April 2005 when vegetation biomass at both sites was about equal.

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**Fig. 6.** Relationship between night-time CO<sub>2</sub> flux (half hour averages) and friction velocity ( $u^*$ ) for July 2005, when highest fluxes were observed (blue circles Stein, red triangles Oukoop).

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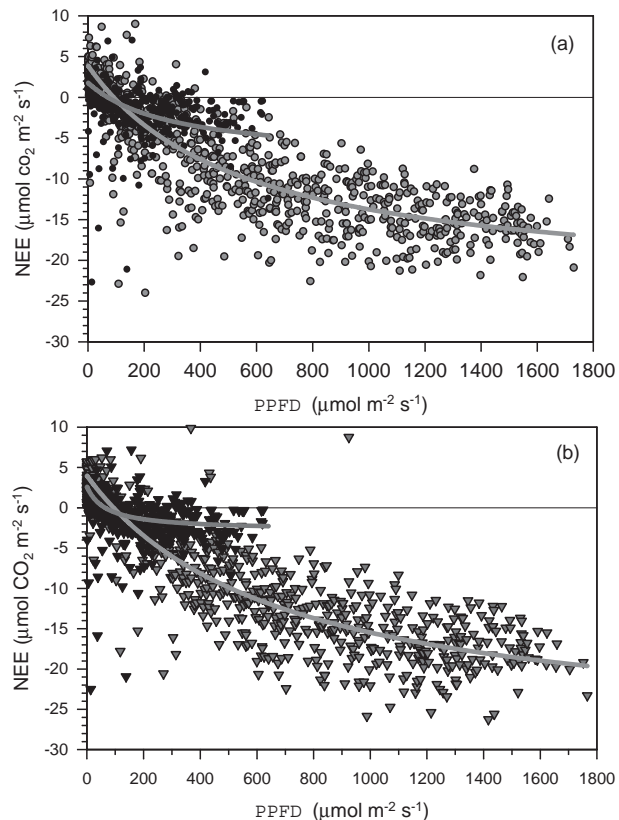
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**Fig. 7.** Relationship between net ecosystem exchange (NEE; half hourly values) and photosynthetic photon flux density (PPFD).

**(a)** Stein (black circles: January; grey circles: April; light grey line: fitted relationship (Eq. 1) for April; dark grey line fitted relationship for January; measurements taken in 2005). **(b)** Oukoop (triangles; legend further as in a).

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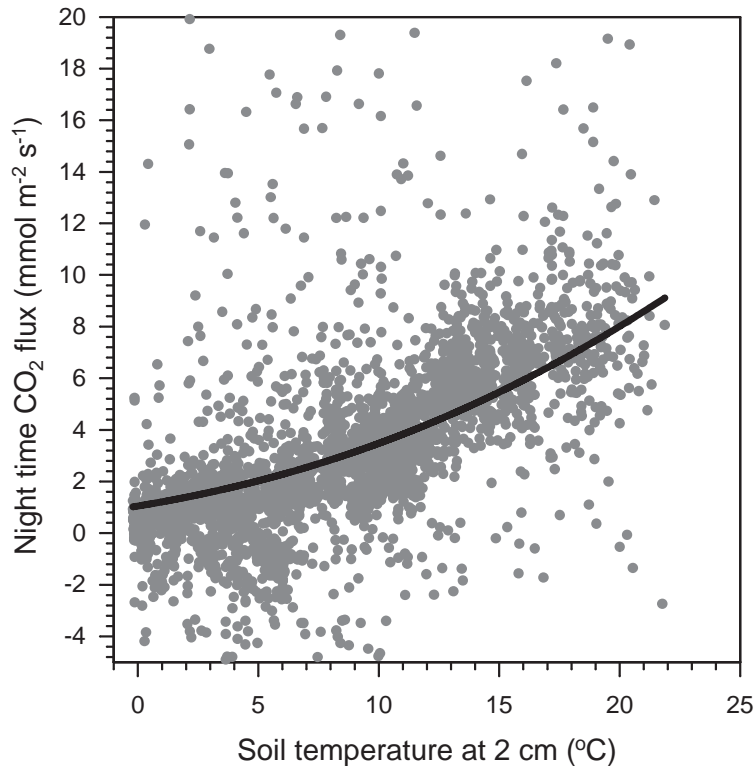
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**Fig. 8.** Relationship between night-time CO<sub>2</sub> flux (grey circles; half hourly averages) and soil temperature (at 2 cm soil depth) for Stein. The solid line denotes the modeled respiration with a Lloyd-Taylor equation ( $R_{10}$  for Stein =  $3.47 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). Measurements from September 2004 to August 2005.

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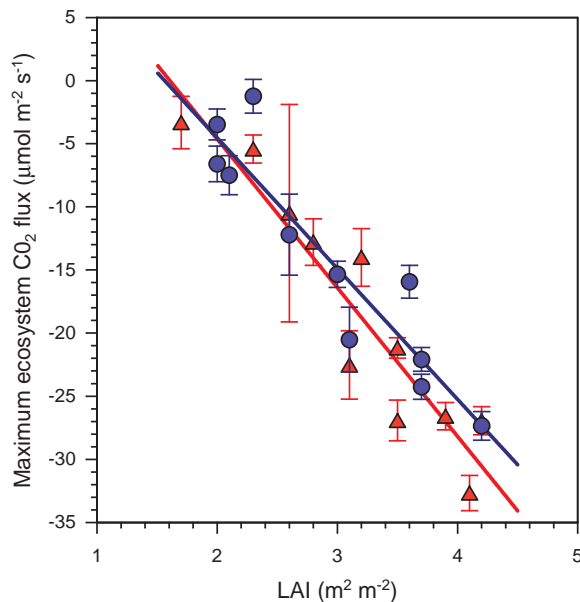
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**Fig. 9.** Relationship between mean leaf area Index (LAI m<sup>2</sup> leaf m<sup>-2</sup> ground surface) and **(a)** and minimum ecosystem flux ( $\beta$ ). (blue circles: Stein; red triangles: Oukoop). Individual regression lines are shown for each site (Mature hay data points in Stein in May and early June were omitted; error bars indicate  $\pm$  one standard error).

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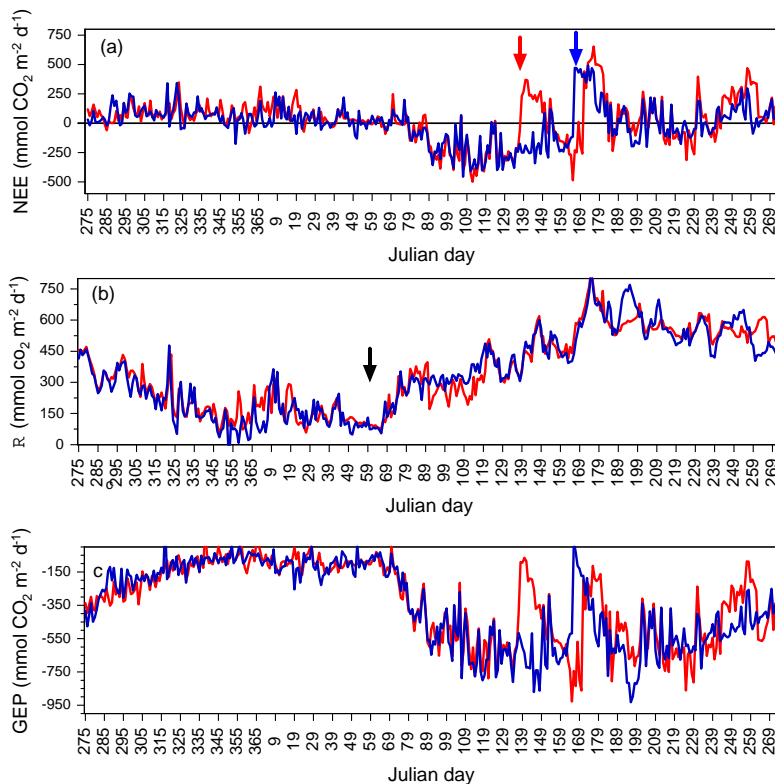
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**Fig. 10.** Seasonal variation in daily values of net ecosystem exchange **(a)**, ecosystem respiration **(b)** and gross ecosystem exchange **(c)**. (Period October 2004 to September 2005; all graphs; Blue line: Stein, extensive management; red line: Oukoop, intensive management). (a) net ecosystem exchange (NEE) (arrows indicate two major grass cutting events in each site.) (b) Ecosystem respiration (*R*) (arrow indicates temperature and respiration increase early March 2005). (c) Gross ecosystem photosynthesis (GEP).

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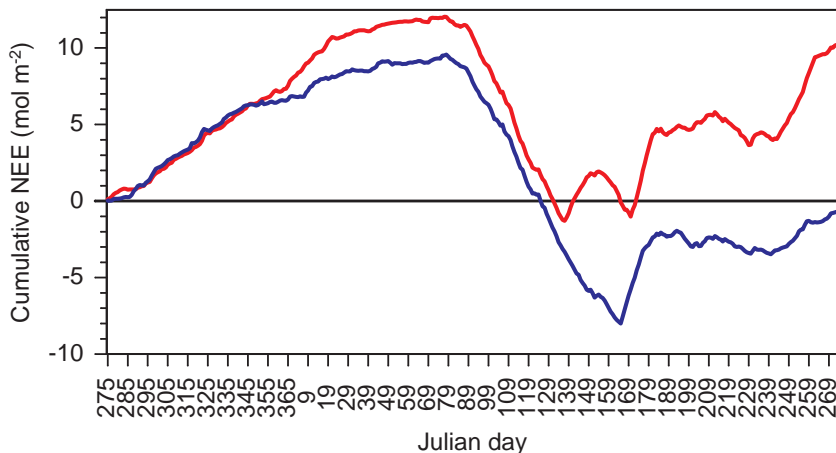
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**Fig. 11.** Annual cumulative net ecosystem exchange (blue line: Stein, extensive management; red line: Oukoop, intensive management). Period October 2004 to September 2005.

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