

## Variability of annual CO<sub>2</sub> exchange from Dutch grasslands

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**Abstract.** An intercomparison is made of the Net Ecosystem Exchange of CO<sub>2</sub>, *NEE*, for eight Dutch grassland sites: four natural grasslands, two production grasslands and two meteorological stations within a rotational grassland region. At all sites the *NEE* was determined during at least 10 months per site, using the eddy-covariance (EC) technique, but in different years. The *NEE* does not include any import or export other than CO<sub>2</sub>. The photosynthesis-light response analysis technique is used along with the respiration-temperature response technique to partition *NEE* into Gross Primary Production (*GPP*) and Ecosystem Respiration (*R<sub>e</sub>*) and to obtain the eco-physiological characteristics of the sites at the field scale. Annual sums of *NEE*, *GPP* and *R<sub>e</sub>* are then estimated using the fitted response curves with observed radiation and air temperature from a meteorological site in the centre of The Netherlands as drivers. These calculations are carried out for four years (2002–2005). Land use and management histories are not considered. The estimated annual *R<sub>e</sub>* for all individual sites is more or less constant per site and the average for all sites amounts to 1390±30 gC m<sup>-2</sup> a<sup>-1</sup>. The narrow uncertainty band (±2%) reflects the small differences in the mean annual air temperature. The mean annual *GPP* was estimated to be 1325 gC m<sup>-2</sup> a<sup>-1</sup>, and displays a much higher standard deviation, of ±110 gC m<sup>-2</sup> a<sup>-1</sup> (8%), which reflects the relatively large variation in annual solar radiation. The mean annual *NEE* amounts to -65±85 gC m<sup>-2</sup> a<sup>-1</sup>. From two sites, four-year records of CO<sub>2</sub> flux were available and analyzed (2002–2005). Using the weather record of 2005 with optimizations from the other years, the standard deviation of annual *GPP* was estimated to be 171–206 gC m<sup>-2</sup> a<sup>-1</sup> (8–14%), of annual *R<sub>e</sub>* 227–247 gC m<sup>-2</sup> a<sup>-1</sup> (14–16%) and of annual *NEE* 176–276 gC m<sup>-2</sup> a<sup>-1</sup>. The

inter-site standard deviation was higher for *GPP* and *R<sub>e</sub>*, 534 gC m<sup>-2</sup> a<sup>-1</sup> (37.3%) and 486 gC m<sup>-2</sup> a<sup>-1</sup> (34.8%), respectively. However, the inter-site standard deviation of *NEE* was similar to the interannual one, amounting to 207 gC m<sup>-2</sup> a<sup>-1</sup>. Large differences occur due to soil type. The grasslands on organic (peat) soils show a mean net release of CO<sub>2</sub> of 220±90 gC m<sup>-2</sup> a<sup>-1</sup> while the grasslands on mineral (clay and sand) soils show a mean net uptake of CO<sub>2</sub> of 90±90 gC m<sup>-2</sup> a<sup>-1</sup>. If a weighing with the fraction of grassland on organic (20%) and mineral soils (80%) is applied, an average *NEE* of 28±90 gC m<sup>-2</sup> a<sup>-1</sup> is found. The results from the analysis illustrate the need for regionally specific and spatially explicit CO<sub>2</sub> emission estimates from grassland.

### 1 Introduction

Grasslands cover about 20% of the world's land area (Hadley, 1993) and about 22% of the EU-25 land area (EEA, 2005). They not only constitute an important socio-economic and environmental resource, but they also affect the atmospheric energy, water and carbon budgets. Currently, it is suggested that grasslands demonstrate the same CO<sub>2</sub> accumulation rates as forests (Hu et al., 2001). If this is correct on a long-term basis, this is of great interest in light of the discussions on global warming. As such, grassland areas contribute significantly to the terrestrial greenhouse gas (GHG) balance (Soussana et al., 2007b). Thus, realistic estimates of greenhouse gas budgets require reliable estimates of emissions from grasslands.

The Net Ecosystem Exchange of CO<sub>2</sub>, *NEE*, usually is the largest component in the surface-atmosphere exchange of GHG at the field scale. It is commonly taken to be the starting

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point in the construction of more complete GHG balances at the farm level (Soussana et al., 2007a) as well as in national GHG inventories (Brandes et al., 2007). Full accounting of the GHG balance then requires to take into account contributions from other GHG, like nitrous oxide and methane, and carbon import and export by management. These contributions may be included as separate subsequent steps in the construction of such a balance (see, Soussana et al., 2007a and Veenendaal et al., 2007 for examples). In this paper, we focus on the first step in the construction of GHG balances of temperate grasslands on regional to national scale, that is, an analysis of the *NEE* of CO<sub>2</sub>.

In national inventory reports such as required under the Kyoto Protocol by the United Nations Framework Convention on Climate Change (UNFCCC) all grasslands are usually shared under one so-called source/removal category with one emission factor (IPCC, 2003). Similarly, in global or regional carbon budget models land cover is often prescribed in terms of biomes such as “temperate grassland” with only one set of vegetation parameters (see, e.g., Friedlingstein et al., 2006). This implies that at regional to national scales, grassland is considered as one homogeneous ecosystem with a single yearly *NEE*. However, even within relatively small regions with uniform climatic conditions large variability in *NEE* from grasslands may be expected due to differences in soil type and water- and land-management practice (Ammann et al., 2007; Gilmanov et al., 2007; Soussana et al., 2007a). Insight into emission variability is necessary to support uncertainty estimates in inventories as well as in modelling studies. Identification of corresponding factors leading to such variability would even more improve the estimate by reducing the uncertainty.

The large variability of CO<sub>2</sub> exchange of grasslands has recently been investigated on a European scale by Gilmanov et al. (2007). These authors compared data from 20 European grasslands, covering a large range of ecophysiological and climatic conditions. Their datasets each represent 1–2 years of flux observations. Annual *NEE* was found to vary between a net uptake of 655 gC m<sup>-2</sup> and a release of 164 gC m<sup>-2</sup>. Net release was observed in 4 cases, associated with organic soils.

In this paper we analyse the CO<sub>2</sub> emission variability of grasslands in The Netherlands. About 50% of the agricultural land in the Netherlands consists of grassland, where rotational grazing is the most common land use (CBS, 2007). Grassland on organic soils plays a special role in the GHG budget from land sources in The Netherlands. A relatively large fraction of about 20% of the production grasslands in The Netherlands is located on peat soils (CBS, 2007). In the national inventory report of The Netherlands grassland is defined as all managed grasslands, natural grasslands and grasslands for recreation. The contribution of grassland to the national greenhouse gas budget is expressed by means of a single emission factor, amounting to 519 gC m<sup>-2</sup> a<sup>-1</sup>. This number includes the emission from drained organic soils

(peat soils). It has been derived from belowground carbon stock changes in such soils, as affected by water management (Brandes et al., 2007). Clearly, this emission factor is much larger than the maximum yearly emission reported by Gilmanov et al. (2007) for organic soils. It neglects inter-annual variability as well as the possible uptake of CO<sub>2</sub> by grasslands on mineral soils and in waterlogged areas. Therefore, while analysing the emission variability of Dutch grasslands, we also attempt to analyse interannual emission variability and the difference in the emission factor between organic and mineral soils.

Emission variability analysis requires continuous observations of GHG exchange during prolonged periods of time and for various sites to address both spatial as well as temporal variability of emission factors. Thanks to the gradually increasing number of sites with long-term flux observations based on the eddy covariance (EC) technique (Baldocchi et al., 2001) such analyses are now within reach for carbon dioxide (CO<sub>2</sub>). In the present study eight datasets of quasi-continuous CO<sub>2</sub> flux measurements covering at least 10 months are analysed. The datasets are all obtained in the past decade, using the EC technique. They represent contrasting grassland sites in The Netherlands, ranging from intensively managed grassland to natural grassland. In contrast with Gilmanov et al. (2007), there is much less variation in the climatic conditions among the sites.

In our analysis, we first investigate CO<sub>2</sub> emission variability by establishing ecophysiological differences between the grasslands, based on the construction of ecosystem response curves, notably the photosynthesis-light and the respiration-temperature response characteristics. The contributions from ecosystem respiration  $R_e$  and photosynthesis (gross primary production, *GPP*) can then be distinguished. To date, this approach is commonly used to analyse *NEE* and has proven to offer a valuable analysis tool for the detection of ecophysiological differences among different locations (Gilmanov et al., 2007). We then estimate annual emissions using data from a meteorological station in the centre of The Netherlands to drive the fitted ecosystem responses of the sites. This methodology may be viewed as a normalisation of the annual CO<sub>2</sub> budget with respect to climatic conditions. It allowed us to better assess the influence of ecophysiological differences between the grasslands, and to pay special attention to the difference between organic and mineral soils. Datasets from two extensively managed grassland sites covered a period of four consecutive years. Based on these data, we also estimated the interannual variability relative to ecophysiological differences.

**Table 1.** Site characteristics of the eight Dutch grassland sites. OC (%) is the organic carbon fraction in the upper 20 cm of the soil.

Name	Type	Soil (FAO)	OC-content (%)	Fertilizer Use	Land Use	Year
Haarweg	WMO-Grassland	Eutric gleyic Fluvisol	3	No	Mowing	2002–2005
Cabauw	WMO-Grassland	Eutric Fluvisol	5	No	Grazing sheep	2002–2005
Horstermeer	Grassland/Wetland	Eutric Histosol	20	No	Semi-natural permanent grassland	2005
Fochterlooërveen	Natural Grassland	Eutric Histosol	50	No	Natural grassland	1994–1995
Haastrecht	Production Grassland	Eutric Fibric Histosol	n/a	Yes	Intensively managed permanent grassland	2003(July)–2004(May)
Oukoop	Production Grassland	Fibric Eutric Histosol	15	Yes	Intensively managed permanent grassland	2005
Stein	Meadow Bird Reserve	Fibric Eutric Histosol	15	No	Natural grassland	2005
Lelystad	Production Grassland	Calcaric Eutric Fluvisol	3	Yes (6 times a year)	Intensively managed permanent grassland	2004

## 2 Materials and methods

### 2.1 Study sites

The Netherlands, a midlatitude coastal country, has a high frequency of rain events that are more or less evenly distributed during the year. The long-term mean precipitation ranges between 730 mm a<sup>-1</sup> (South West) and 750 mm a<sup>-1</sup> (East) and occurs during 190±26 days a year (Jacobs et al., 2006). The long-term mean annual temperature ranges between 8.9°C (North) and 9.5°C (South) and the long-term mean incoming solar radiation ranges between 3400 MJ m<sup>-2</sup> a<sup>-1</sup> (Centre) and 3850 MJ m<sup>-2</sup> a<sup>-1</sup> (West).

CO<sub>2</sub> exchange of 8 grassland sites distributed over the Netherlands is analyzed. The geographical locations of these sites are shown in Fig. 1. All sites have a so-called long potential growing season (above 260 days), in which the mean air temperature is above 5°C. For example, the most eastern and coldest grassland site had a potential growing season of 305±12 days in the years 2002–2005, which is the period analyzed here.

In order to measure the CO<sub>2</sub> fluxes, all stations are equipped with EC systems, consisting of a fast response sonic anemometer and a fast response CO<sub>2</sub> – H<sub>2</sub>O analyzer. General principles of the EC flux measurement methodology as well as processing of the data required to obtain high-quality flux estimates are described by Aubinet et al. (2000, 2003). For all sites included in this study, data treatment and quality control closely followed the guidelines in these papers.

In addition to the EC devices at each site a weather station is installed, which provides 30-min averages of global radiation ( $R_{in}$ ), net radiation, air temperature ( $T_a$ ), vapour pressure, wind speed, wind direction and precipitation. The agro-meteorological station “Haarweg” in the centre of the Netherlands is equipped with an independent double meteorological measurement system in order to avoid gaps in the data. This makes the meteorological data from this station

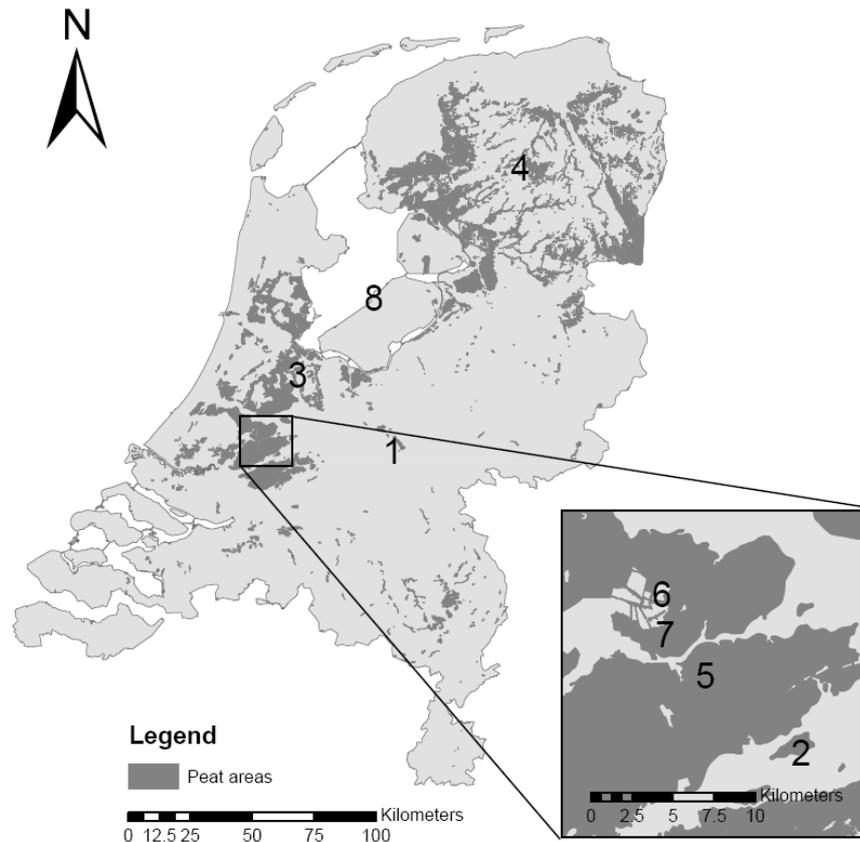
suitable to estimate annual CO<sub>2</sub> budgets from the ecosystem responses (see Sects. 2.2 and 2.3).

Below a brief description is given of the various grassland sites included here. Moreover, the main characteristics of the sites are listed in Table 1. For more detailed information on the EC measurements, the reader is referred to the cited literature.

#### 2.1.1 Haarweg station

The meteorological observatory of the Wageningen University, Haarweg Station, is located in the centre of the Netherlands (lat. 51° 58' N, long. 5° 38' E, altitude +7 m a.s.l.; www.met.wau.nl). The dominating plant species in this perennial grassland area are rye grass (*Lolium perenne*) and rough blue grass (*Poa trivialis*). The soil at the site is predominantly heavy clay resulting from the back-swamps of the river Rhine.

Because the site is a meteorological station, the one-sided Leaf Area Index, *LAI*, of the terrain is kept constant as good as possible and has a numerical value of 2.9±0.3. Because there is a unique relation between the grass height and *LAI* (Keuning, 1988), this is done by checking the mean grass height (about 10 cm) daily, with a special grass height meter (Eijkelkamp, model NMI). About monthly the *LAI* is measured by a plant analyzer (CID-Inc. model CI-110). During the growing season (1 May–1 November), the grass cover is mowed weekly, but keeping the minimum required *LAI* of 2.6. If the *LAI* as derived from the observed grass height exceeds the maximum value of 3.2 within a week, the grass is mowed more frequently. At the measurement site the mowed grass is not removed but evenly spread over the area. CO<sub>2</sub> flux measurements from the period 2002–2005 are analyzed here. More details about the site can be found in Jacobs et al. (2003a).



**Fig. 1.** Geographical distribution of the Dutch grassland study sites: 1 – Haarweg, 2 – Cabauw, 3 – Horstermeer, 4 – Fochteloöerveen, 5 – Haastrecht, 6 – Oukoop, 7 – Stein, 8 – Lelystad. Shaded areas denote peat soils.

### 2.1.2 Fochteloöerveen

The Fochteloöerveen area is a disturbed raised bog in the north of the Netherlands (lat. 53° 00' N, long. 6° 24' E, altitude +11 m a.s.l.). The vegetation is a natural tussock grassland, with an average height of approximately 0.4 m. A layer of 0.1 m of dead organic material from the previous growing seasons covered the tussocks and the hollows in between. The dominating plant species is *Molina caerulea* (>75%) but also species like *Eriophorum vaginatum*, *Calluna vulgaris* and *Erica tetralix* could be found. The green LAI has a maximum of about 1.7 in August. Throughout the seasons, the water table depth varied, depending on the weather, from 0 to 0.2 m below the tussock soil interface but the soil remained saturated. CO<sub>2</sub> fluxes were measured between June 1994 and October 1995. More details about this site can be found in Nieveen et al. (1998) and Jacobs et al. (2003b).

### 2.1.3 Cabauw

The Cabauw site is located on grassland in the centre of the Netherlands (lat. 51° 57' N, long. 4° 54' E, altitude – 0.7 m a.s.l.). The dominating plant species in this perennial

grassland area are *Lolium perenne* (40%), *Poa trivialis* (20%) and *Alopecurus geniculatus* (10%). The grass is maintained by grazing of sheep and the mean LAI is about 3. The soil is a 0.7 m thick clay layer on peat. Ditches occupy 10% of the aerial surface. The water level in the ditches is kept constant during the winter half year and the summer half year respectively. Horizontal transport of water from the grassland to the ditches is limited. This results in considerable changes in ground water level at the central parts of the grassland throughout the year.

CO<sub>2</sub> fluxes from four consecutive years (2002–2005) are analysed here. With westerly wind, the footprint of the flux observation is partly over a neighbouring field which is bare soil in winter and maize during summer. Results from the wind direction from this area, between 177 and 317 degrees, are therefore ignored in the present study. More details about this site can be found in Beljaars and Bosveld (1997).

### 2.1.4 Horstermeer

The Horstermeer site is a grassland/wetland polder of a former agricultural land in a drained natural lake in the centre of the Netherlands (lat. 52° 02' N, long. 5° 04' E, altitude –

2.2 m a.s.l.). The site has been taken out of agricultural production more than 10 years ago, and has developed into semi-natural grassland. The two meter thick soil consists of peat, overlain with organic-rich lake deposits and is overlying eolian sands of Pleistocene age. After the site has been taken out of agricultural production, the ditch water table has been raised to approximately 10 cm below the land surface. Large parts of the Horstermeer polder are subject to strong groundwater seepage from surrounding lake areas and Pleistocene ice pushed ridges. At the measurement location seepage is largely reduced and even infiltration occurs as a result of the high water table. The surface of the research area consists for 10% of ditches, for 20% of land that is saturated year-round (mostly alongside the ditches) and for 70% of relatively dry land with a fluctuating water table (between 0 to 40 cm below the soil surface) and an aerated top-layer. Management consists only of regulation of the ditch water table; no cattle grazing or harvesting takes place, the only removal of vegetation consists of sporadic grazing by roe deer. Vegetation consists of different types of grasses (dominant species *Holcus lanatus*, *Phalaris arundinacea*, *Glyceria fluitans*), horsetail (*Equisetum palustre*, *fluviatile*) reeds (*Phragmites australis*, *Typha latifolia*) and high forbs (*Urtica dioica*, *Cirsium arvense*, *palustre*). Measurements of CO<sub>2</sub> fluxes from the year 2005 are included in the present study. More details about this site can be found in Hendriks et al. (2007).

### 2.1.5 Haastrecht

The Haastrecht site is a grassland polder in the centre of the Netherlands (lat. 52° 00' N, long. 4° 48' E, altitude -1.4 m a.s.l.). The dominating plant species in this perennial grassland area are *Lolium perenne* and *Poa trivialis*. The soil at the site is predominantly a peat soil. The water table is kept constant with a level of -1.6 m during the summer season and -1.8 m during the winter season. The grass at the measurement site is maintained by grazing of sheep.

CO<sub>2</sub> flux measurements were performed from July 2003 until May 2004. Eddy covariance devices were mounted at a height of 4 m. Windspeed was measured using a sonic anemometer (Gill R3-50). Air temperature was also derived from this instrument. CO<sub>2</sub> concentration was measured with an open path H<sub>2</sub>O/CO<sub>2</sub> sensor (LICOR, Li-7500). Supporting measurements include observations of incoming short-wave radiation, using a pyranometer (Kipp & Zonen, CM21). The direct surroundings of the measurement site are agricultural grasslands with rotational grazing by cows and sheep. The fetch in the direction of the prevailing winds (South-West to West) is about 5 km.

### 2.1.6 Stein

The Stein site is a polder in the west of the Netherlands (lat. 52° 01' N, long. 4° 46' E, altitude -1.6 m a.s.l.). The polder was used as grass production land and during the past

20 years the area has gradually become a meadow bird reserve. The dominating plant species in this perennial grassland area are *Lolium perenne* and *Poa trivialis*. Vernal grass (*Anthoxanthum odoratum*) and sour dock (*Rumex acetosa*), however, are becoming more abundant. The soil at the site is a clayey peat or peaty clay of about 25 cm thickness on a 12 m thick peat layer. About 15% of the area is open water (ditches or low parts in the landscape). CO<sub>2</sub> flux measurements were conducted from 2004 onwards. More details about this site can be found in Veenendaal et al. (2007).

### 2.1.7 Oukoop

The Oukoop site is a grassland polder in the west of the Netherlands (lat. 52° 02' N, long. 4° 47' E, altitude -1.8 m a.s.l.). The grassland site is part of an intensive dairy farm with rotational grazing during the summer period (mid-May–mid-September). The dominating plant species in this perennial grassland area are *Lolium perenne* and *Poa trivialis*. Manure and fertilizers are applied two or three times a year, but not during winter time. The area is about 4 km South-West of the Stein location and has the same soil characteristics. CO<sub>2</sub> flux measurements started in 2004. More details about this site can be found in Veenendaal et al. (2007).

### 2.1.8 Lelystad

The Lelystad site is a grassland site in the centre of the Netherlands (lat. 52° 31' N, long. 5° 35' E, altitude 0 m a.s.l.). The site is located in the Flevopolder, an area reclaimed from Lake IJssel in 1965. The soil consists of young sea clay. The groundwater table is maintained at about 1 m below the ground surface, but it can be higher during periods of rain. The grassland site is part of an experimental farm “De Wai-boerhoeve” with intensive management with 5-6 harvests a year. Grass was removed from the field either by cutting or by grazing. The farm has a total number of 400 cows and 500 sheep. Manure and fertilizers are applied about six times a year, but not during winter time. CO<sub>2</sub> flux observations from the period July 2003 until June 2004 are analyzed here. More details about this site can be found in Gilmanov et al. (2007).

## 2.2 Net Ecosystem Exchange (*NEE*) and Ecosystem Respiration (*R<sub>e</sub>*)

The Net Ecosystem Exchange, *NEE*, is the result of photosynthetic uptake, *GPP*, and the ecosystem respiration, *R<sub>e</sub>*. Using the ecological sign convention with photosynthetic uptake defined positive, we have:

$$NEE = GPP - R_e \quad (1)$$

During nighttime, only respiration occurs which enables analyses based on a distinction between daytime (downward

solar radiation ( $R_{in}>0$ ) and nighttime ( $R_{in}=0$ ) fluxes. For nighttime Eq. (1) reduces to:

$$NEE = -R_e = -R_{\text{night}} \quad (2)$$

Temperature is an important driving variable of respiration. This relation is usually expressed by means of, for example, an Arrhenius-type relation. Here, we apply the following equation to analyze the response of respiration to temperature (Lloyd and Taylor, 1994):

$$R_e = R_{10} \exp\left(E_a \left(\frac{1}{10 - T_0} - \frac{1}{T - T_0}\right)\right) \quad (3)$$

where  $R_{10}$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) is the reference respiration at a reference temperature of 10°C (the numerical value appearing in the equation),  $T$  (°C) is temperature,  $E_a$  (K) is the so-called ecosystem activation energy or sensitivity coefficient, and  $T_0 = -46.02^\circ\text{C}$  is the zero respiration temperature, denoting the temperature below which there is no respiration anymore. Temperature  $T$  in (3) may be soil temperature  $T_s$  or air temperature  $T_a$ . Usually,  $T_s$  is chosen to be the driving variable in (3). However,  $R_e$  originates from the soil and the vegetation, representing a complex interplay between various aboveground and belowground processes. Photosynthesis and some of the processes contributing to ecosystem respiration may be intimately linked at various time and spatial scales (Hartley et al., 2006). Because photosynthesis is driven by aboveground temperatures, it need not be surprising that the fraction of variance in  $R_e$  explained by (3) using either  $T_a$  or  $T_s$  does usually not differ much. For forest in particular, even slightly better correlations have been reported using  $T_a$  (Reichstein et al., 2005; Ruppert et al., 2006). Moreover, Van Dijk and Dolman (2004) found that using  $T_a$  gives much more consistent results in inter-site comparisons, which they suggested to be due to problems and inconsistencies in the measurement of  $T_s$ . Although they analysed  $R_e$  of forest, the latter argument applies to other ecosystems as well. Because of the aforementioned arguments we decided to use  $T_a$  instead of  $T_s$ . In contrast with  $T_a$  that is readily observed,  $T_s$  is not available at all sites. Therefore, using  $T_a$  assures an analysis that is similar for all sites, that is, an analysis based on the same driving variables for all sites.

From the nighttime flux data we excluded those obtained during precipitation events. Furthermore, it was required that friction velocity  $u_* > 0.1 \text{ m s}^{-1}$ . During relatively calm stable nights turbulence is suppressed and the eddy-covariances become ill-defined since these conditions are non-stationary and non-homogeneous. It appears that the criterion  $u_* \leq 0.1 \text{ m s}^{-1}$  is an appropriate threshold for not applying the eddy-covariance technique (Van de Wiel et al., 2003). Indeed, analysis of the Haarweg data showed that the uncertainty in  $R_e$  due to uncertainty in the fitted parameters was less than 3% for 3 out of 4 years as long as  $u_* > 0.1 \text{ m s}^{-1}$ , but only increased to about 7% in one case (2003).

To determine the responses of  $R_e$  to temperature, the data from one entire year were averaged in  $T_a$  bins with an equal number of data. Equation (3) was then fitted to the bin averages, by optimizing the reference respiration,  $R_{10}$  as well as  $E_a$  (Ruppert et al., 2006). Annual sums of the respiration are then estimated by applying Eq. (3), with observed  $T_a$  from Haarweg as the driving variable.

The base respiration  $R_{10}$  and sensitivity coefficient  $E_a$  are probably influenced by soil moisture as well (Reichstein et al., 2005). Similarly, changes in ecosystem characteristics may affect  $R_e$ . To deal with these effects, the optimization may be carried out for separate, shorter periods of time. Tests with separate optimizations per period of half a month for the year 2005 showed that the effect on the annual sums of  $R_e$  varies from minor ( $48 \text{ gC m}^{-2} \text{ a}^{-1}$  or 3% in the case of Cabauw) to considerable ( $205 \text{ gC m}^{-2} \text{ a}^{-1}$  or 22% in the case of Lelystad). However, the numbers are then based on sometimes meaningless fits, with negative or very low correlations between model and data, with sometimes spurious behavior of  $R_{10}$ . Furthermore, for some sites gaps of a few months per year occurred, which implies additional uncertainty in inter-site comparisons, with results that cannot be compared anymore. Considering our goal, that is, to provide an estimate of the differences at an annual basis, it may therefore be argued that such a refined analysis does not necessarily imply a more reliable result. Therefore, it was decided to restrict our analyses to periods of one entire year.

### 2.3 Photosynthetic uptake (GPP)

There are two major light-use efficiency characteristics used in literature; the physiological one and the ecological one. Here we use the ecological light-use efficiency because these characteristics match the scale of our analysis (Gilmanov et al., 2007). The daytime data ( $R_{in}>0$ ) are used to make an assessment of the light-response curves at the ecosystem scale. Again, data during episodes of precipitation are discarded. The data were stratified in  $T_a$  classes of 5°C and per temperature class the data were binned into 10 light intensity classes of equal numbers of data. Light response curves were then fitted to the light-bin averages, using the rectangular hyperbola (Goudriaan and Van Laar, 1994):

$$NEE + R_e = GPP = \frac{\alpha R_{in} GPP_{\text{max}}}{\alpha R_{in} + GPP_{\text{max}}} \quad (4)$$

where  $R_{in}$  ( $\text{W m}^{-2}$ ) is the incoming short wave radiation,  $\alpha$  ( $\mu\text{mol J}^{-1}$ ) is the actual light conversion factor and  $GPP_{\text{max}}$  ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) is the maximum gross assimilation rate.  $GPP_{\text{max}}$  is an asymptotic value that varies during the seasons and for different ecosystems. However, it often does not saturate within a realistic range of radiation intensities, especially in cases where the response tends to be linear, or if no observations are available beyond the quasi-linear section of the curves. In such cases, the fitted  $GPP_{\text{max}}$  is not a realistic measure of maximum gross assimilation rates. Therefore, in

order to obtain a more realistic comparison between different sites we follow Ammann et al. (2007) and use  $GPP_{1000}$  instead. This parameter denotes the gross assimilation rate at a solar light intensity of  $R_{in}=1000\text{ W m}^{-2}$ , derived from the fitted response function (4). As such,  $GPP_{1000}$  can be interpreted as a measure of the so-called light saturation point for the various ecosystems. An alternative would be to reformulate (4) in terms of  $GPP_{1000}$  (Falge et al., 2001).

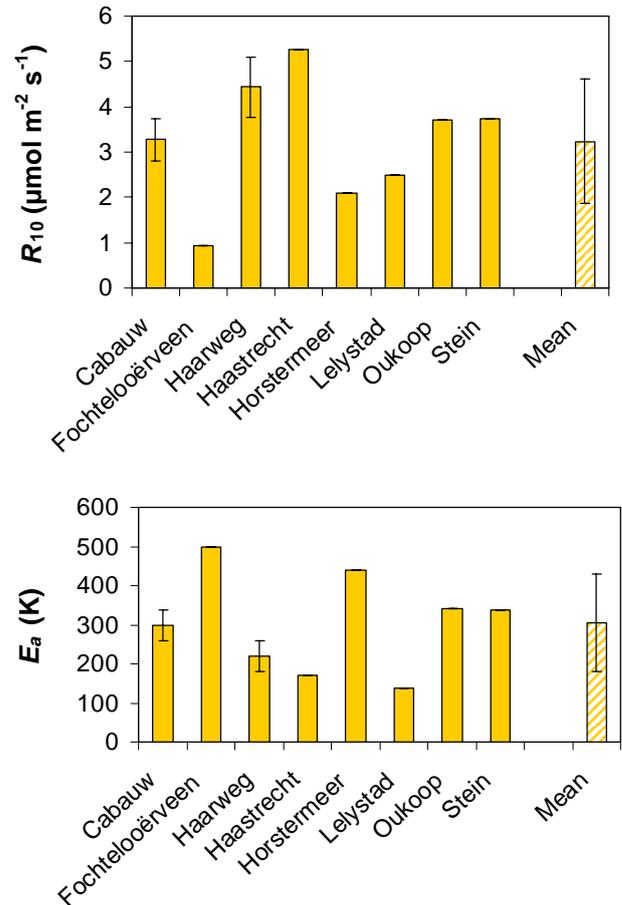
The stratification in temperature classes accounts for the effect of temperature on the photosynthesis. In addition photosynthesis may be affected by the humidity of the air, due to stomatal closure under dry atmospheric conditions. However, humidity deficit and temperature are strongly correlated in particular at the upper temperature ranges above the photosynthetic temperature optimum. Consequently, at the ecosystem scale, accounting for humidity differences as well has only a small effect on the annual sums in practice, in particular if the temperature bins are reduced. Similarly, as suggested by Ruppert et al. (2006) ecosystem characteristics affecting the light response may be correlated with temperature at seasonal timescales. In particular LAI may have an impact on the light response of the grasslands, which appears to be a linear impact for the Stein and Oukoop sites (Veenendaal et al., 2007). Therefore, at sites with significant cuts in LAI that are independent of temperature we assumed that only the uncertainty of the average light response curves will be increased. However, at the longer timescales considered here, for sites with less intensive management, LAI may also show some correlation with temperature as well. Yet some other sites have almost constant LAI at seasonal time scales. Therefore, and because our data did not allow further stratification in LAI for all the sites, we decided to only stratify our data in temperature classes. Tests were performed with temperature bins reduced to 2 K. The scatter in the fitted parameters increased, but differences of <1% ( $\sim 15\text{ gC m}^{-2}\text{ a}^{-1}$ ) were found with respect to the annual sums of  $GPP$ . Therefore,  $T_a$  bins of 5 K were used.

### 3 Results and discussion

#### 3.1 Respiration characteristics

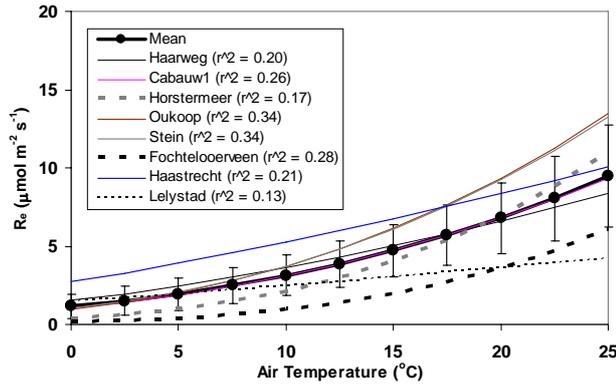
First, the nighttime fluxes of all grassland stations are analyzed in order to obtain the reference respiration,  $R_{10}$ , and the activation energy,  $E_a$ . Figure 2 shows the results from this analysis for the individual sites, as well as the mean parameter value from all the sites. In the case of Haarweg and Cabauw, the mean of 4 years has been plotted. Error bars denote the standard deviation.

It can be seen that the Stein and Oukoop locations behave more or less similar in their respiration characteristics. Both stations are situated in the same area and have nearly the same history. Only during the past 20 years the Stein site is gradually subjected to a changing management



**Fig. 2.** The reference respiration,  $R_{10}$ , and the ecosystem activation energy,  $E_a$ , for the various grassland stations. For the Haarweg and Cabauw sites, the standard deviations have been indicated for the four measurement years.

regime, from intensively managed grassland into a meadow bird reserve. Apparently, this change has hardly affected the respiration characteristics until today. Second, we infer from Fig. 2 that the Fochteloërveen and Horstermeer grassland/wetland locations deviate most from all other locations. The Fochteloërveen area is a natural bog area. In summertime only, there is green vegetation with a very low LAI (about 1.7) and with a relatively high water table ranging between  $-0.0\text{ m}$  (wintertime) and  $-0.2\text{ m}$  (summertime) below the tussock soil interface. The Horstermeer area is a grassland/wetland area that is taken out of production for more than 10 years and has been developed into a semi-natural grassland/wetland. Also here the water table is relatively high and ranges between  $-0.4$  (summertime) and  $-0.0\text{ m}$  (wintertime). As a consequence, at both locations the aeration of the uppermost soil layer is probably reduced, which then limits the respiration. In peat areas where the water table is usually close to the ground surface, this phenomenon may then result in a close relation between the water table

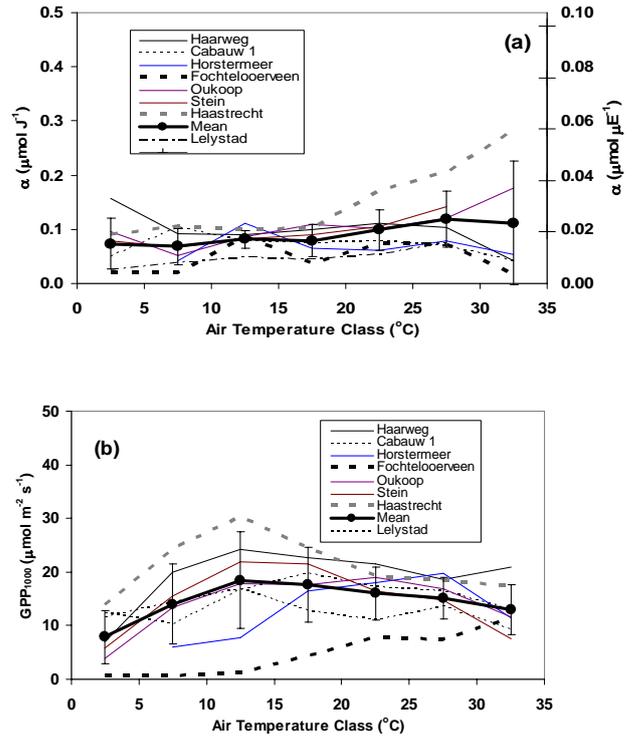


**Fig. 3.** The air temperature dependency of the respiration of all grassland locations along with the averaged values and standard deviations. For each site, the goodness of fit ( $r^2$ ) of the respiration model (3) to the individual data points has been indicated in the legend ( $r^2$ ).

depth and respiration (Lloyd, 2006). In places with a less direct coupling between soil moisture content of the upper layer and the depth of the groundwater table, such a relation may be very weak or absent (Lafleur et al., 2005; Nieveen et al., 2005).

For the Haarweg and Cabauw sites, observations from four complete years (2002–2005) are available. To get insight into the interannual variation of  $R_{10}$  and  $E_a$ , their standard deviations have been calculated for both sites and plotted in Fig. 2 as well. These standard deviations can then be compared with the standard deviation from the average of all sites. In the case of Haarweg, the standard deviation in  $R_{10}$  amounts to  $0.66 \mu\text{mol m}^{-2} \text{s}^{-1}$  (15% of the average from four years), while it is 39 K in  $E_a$  (18%). For Cabauw, the standard deviations are  $0.46 \mu\text{mol m}^{-2} \text{s}^{-1}$  (14%) and 39 K (13%), respectively. This is much less than the standard deviations from all sites:  $1.37 \mu\text{mol m}^{-2} \text{s}^{-1}$  for  $R_{10}$  (31%) and 125 K (41%) for  $E_a$ , respectively. Assuming similar variability characteristics for all sites, these estimates of interannual variability imply an error of  $\sim 15\%$  in estimates of annual respiration if we apply the respiration characteristics calculated from 1 year observations to all other years (also see Sect. 3.3).

To have some idea of the mutual respiration differences between all eight grasslands, the fitted respiration curves of all sites have been plotted in Fig. 3 as function of the air temperature along with the averaged temperature dependency and their standard deviations. The goodness of fit of the respiration model (3) to the individual datapoints, indicated in the legend of Fig. 3, is rather low. Apart from the fact that the low  $r^2$  values may reflect some uncertainty in the measurements, this is also assumed to be related to the fact that factors other than temperature, such as soil moisture, probably exert important controls on respiration as well. Yet, the fits to the smoothed functions were quite reasonable (with  $r^2$  between 0.80 and 0.96, except for Lelystad where  $r^2=0.58$ ),



**Fig. 4.** The air temperature dependency of the light conversion factor,  $\alpha$ , (top frame) and gross assimilation rate at an incoming short wave radiation of  $1000 \text{ W m}^{-2}$ ,  $GPP_{1000}$ , (bottom frame) of all grassland locations along with the averaged value and their standard deviations.

showing that on average and for the purpose of constructing annual sums the respiration model (3) may perform quite satisfactorily.

Clearly, it can be inferred from Fig. 3 that both grassland/wetland locations, Horstermeer and Fochteloöerveen, reveal relatively low respiration rates at low temperatures, but their high temperature sensitivity compensates for the lower base respiration at the higher temperatures. Considering the response curves over the entire range, these two sites cause the relatively large standard deviations from the mean value. Moreover, from Fig. 3 it can be observed that the Haastrecht site shows a relatively high base respiration rate. The Haastrecht site is a peat soil area and has a lower water table than the Fochteloöerveen and Horstermeer sites which ranges between  $-0.2$  (summertime) and  $-0.4$  m (wintertime). Probably both reasons (peat soil and lower water table) are responsible for the relatively high base respiration rate at the Haastrecht site. However, the temperature sensitivity is much less than at Horstermeer and Fochteloöerveen, which tends to reduce the overall respiration rate at the higher temperatures. The Lelystad site reveals a similar low temperature sensitivity. However, in this case the base respiration is much like the average one, resulting in relatively large deviations from the average at higher temperatures.

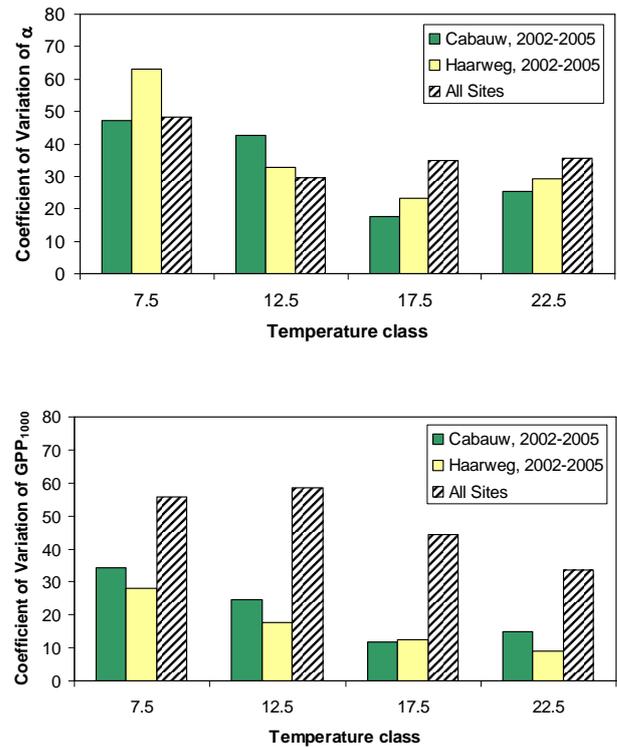
### 3.2 Light responses

Figure 4 depicts the characteristics of the light response curves of all eight grassland sites as a function of the temperature. The temperature taken is central in the 5-degree temperature bins defined in the analysis. This is very close to the bin-averaged temperature. In the case of Cabauw and Haarweg, the values from 2005 have been plotted. The variability of the parameters during the period 2002–2005 will be further investigated below.

In the top panel of Fig. 4, all the light conversion factors  $\alpha$  are plotted along with the average from all sites and the standard deviations per temperature bin. It can clearly be seen that on average  $\alpha$  is nearly a constant for all temperature classes, with a value somewhat below  $0.1 \mu\text{mol J}^{-1}$ . The Fochteloërveen area has a very low LAI, especially during the start and the end of the growing season ( $\text{LAI} < 1$ ). It must be expected that this is the reason for a relatively low light conversion factor for this area in particular for the low temperature classes. On the other hand,  $\alpha$  at the Haastrecht site is rather high at higher temperatures. This causes the largest part of the standard deviation in the temperature classes  $> 20^\circ\text{C}$ . Since the Haastrecht site generally also shows the highest values of the gross maximum assimilation rate (see below) this may be an effect of a high LAI in this area. Effects of LAI on the light conversion factor and on the assimilation rate at saturating light intensity has been demonstrated at the Oukoop and Stein sites by Veenendaal et al. (2007). However, note that part of the large standard deviation at high temperatures is due to uncertainty in the fits caused by low numbers of data in these temperature classes.

The bottom panel of Fig. 4 shows the gross assimilation rate at a solar light intensity of  $R_{in} = 1000 \text{ W m}^{-2}$ ,  $GPP_{1000}$  as derived from the fitted response functions. It must be expected that for an ecosystem with a low LAI, the light saturation is reached at lower irradiation than for an ecosystem with a high LAI (Goudriaan and Van Laar, 1994) and  $GPP_{1000}$  will be higher for ecosystems with higher LAI. Figure 4 clearly reflects that for the Fochteloërveen site, which has the lowest maximum LAI ( $\text{LAI}_{\text{max}} \approx 1.7$ ). Similarly, Haastrecht presumably has the highest LAI. Although there are no direct observations, at locations near the Haastrecht site LAI values up to about 10 have been observed.

Observations from four complete years (2002–2005) at Haarweg and Cabauw are further analyzed to get insight into the interannual variation of  $\alpha$  and  $GPP_{1000}$ , relative to the variation between sites. We consider the temperature classes between 5 and  $25^\circ\text{C}$  because the fits in these classes are most reliable and are available for all years. These variations can then be compared with the standard deviation from the average of all sites. Figure 5 shows as a function of the middle temperature of the bins the coefficient of variation (CV, standard deviation relative to the mean value) of  $\alpha$  and  $GPP_{1000}$  for the Haarweg and Cabauw averages in the period 2002–2005, and for the individual years of all sites (2005 in the



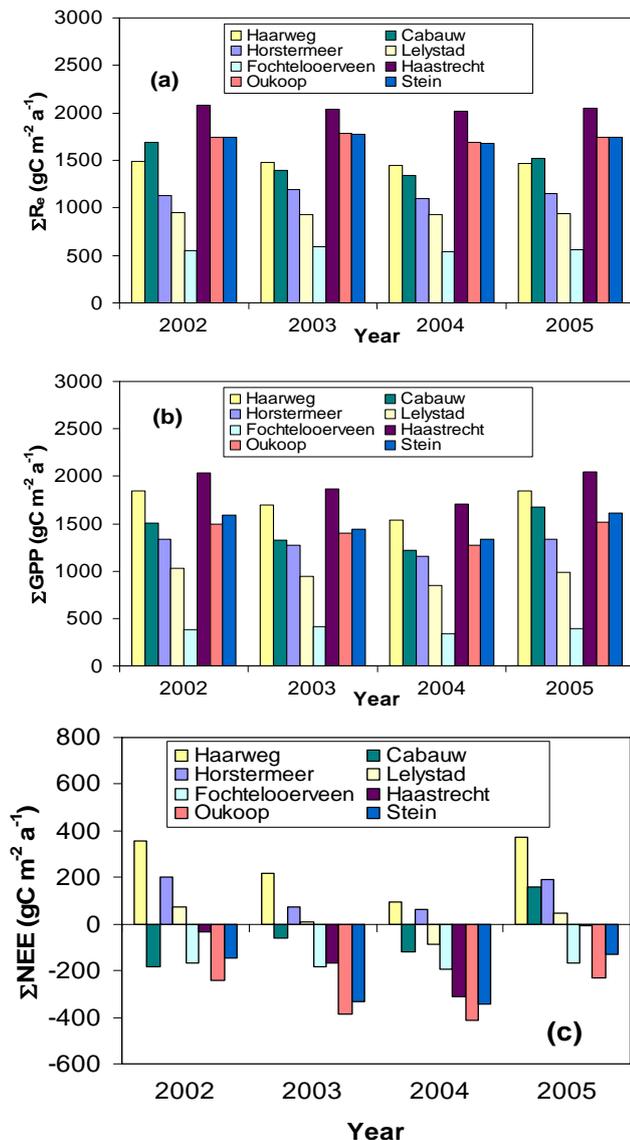
**Fig. 5.** Coefficient of variation per temperature class of  $\alpha$ , (upper frame) and  $GPP_{1000}$  (lower frame). The temperature class is indicated by the middle temperature of the class. The CV from of interannual variability (Haarweg and Cabauw, 2002–2005) is compared to CV from the intersite variability (year 2005).

case of Haarweg and Cabauw). The interannual variability of  $\alpha$  is comparable or even larger than the inter-site variability, with CV values between 18 and 63%. In contrast, the interannual variability of  $GPP_{1000}$  is clearly less than the inter-site variability. CV values range between 12 and 35% for the interannual variability, and between 34 and 59% for the inter-site variability. At the lower and higher  $T_a$  classes, the uncertainty tends to be larger because there are less data in the bins. Also, because temperature and irradiation are correlated, high  $R_{in}$  is underrepresented at low  $T_a$  and the reverse.

Because the values of  $\alpha$  and  $GPP_{\text{max}}$  (or  $GPP_{1000}$ ) from the fits tend to be negatively correlated, the estimated variability in the annual  $GPP$  is much less. Based on the observed meteorological conditions at Haarweg in the year 2005, the CV of annual  $GPP$  amounts to about 9 and 14% for Haarweg and Cabauw, respectively, while it is nearly 38% for the inter-site variability. Thus, again assuming similar variability characteristics for all sites, these estimates imply an error of  $\sim 15\%$  in estimates of annual  $GPP$  if we apply the light-response characteristics calculated from 1 year of observations to all other years (also see Sect. 3.3).

**Table 2.** Estimated mean and standard deviation of annual *GPP*, *R<sub>e</sub>* and *NEE* for all sites in the year 2005 and for Haarweg and Cabauw over the period 2002–2005.

	<i>R<sub>e</sub></i> (gC m <sup>-2</sup> a <sup>-1</sup> )	$\sigma R_e$ (gC m <sup>-2</sup> a <sup>-1</sup> )	<i>GPP</i> (gC m <sup>-2</sup> a <sup>-1</sup> )	$\sigma GPP$ (gC m <sup>-2</sup> a <sup>-1</sup> )	<i>NEE</i> (gC m <sup>-2</sup> a <sup>-1</sup> )	$\sigma NEE$ (gC m <sup>-2</sup> a <sup>-1</sup> )
Cabauw (2002–2005)	1458	227 (15.6%)	1466	206 (14.1%)	8	276 (3422%)
Haarweg (2002–2005)	1803	247 (13.7%)	2011	171 (8.5%)	208	176 (84.8%)
All sites (2005)	1396	486 (34.8%)	1432	534 (37.7%)	36	207 (575%)

**Fig. 6.** The individual cumulative *R<sub>e</sub>* (a), *GPP* (b) and *NEE* (c) of all grassland stations for 2002 until 2005.

### 3.3 Annual CO<sub>2</sub> exchange

Figure 6 contains the individual annual sums of *R<sub>e</sub>*, *GPP* and *NEE* for the eight different locations and the four selected years. The sums have been computed using the observed meteorological conditions (*T<sub>a</sub>* and *R<sub>in</sub>*) at Haarweg as driver of the response functions. Because the response functions used are the same in each year, the interannual variability revealed in Fig. 6 reflects differences in the main climatological drivers.

The respiration does not show large interannual differences for all eight individual sites. This is to be expected because the driving variable of the respiration model is *T<sub>a</sub>*, which does not vary much on the annual timescale, in the period considered here. For example, at the Haarweg site the long-term mean annual air temperature is  $9.4 \pm 0.7^\circ\text{C}$  (Jacobs et al., 2006). The average *R<sub>e</sub>* for all sites is  $1390 \pm 30 \text{ gC m}^{-2} \text{ a}^{-1}$ , where the  $\pm$  ranges mean the intersite variability. The average *GPP* for all sites amounts to  $1325 \pm 110 \text{ gC m}^{-2} \text{ a}^{-1}$ , which displays a much higher variability (8%) than the respiration (3%). *GPP* depends on *R<sub>in</sub>* in combination with *T<sub>a</sub>*. In particular *R<sub>in</sub>* can vary much between the years. For example, the long-term *R<sub>in</sub>* for the Haarweg site is  $3400 \pm 300 \text{ MJ m}^{-2} \text{ a}^{-1}$ .

Obviously, the *NEE*, being the difference of *GPP* and *R<sub>e</sub>*, shows a much larger variation (see Fig. 6c). On average, the annual *NEE* amounts to  $-65 \pm 85 \text{ gC m}^{-2} \text{ a}^{-1}$ , which means that on average our grasslands emit CO<sub>2</sub>, with a relatively large standard deviation.

We next assess the interannual variation of the carbon exchange components due to eco-physiological differences (see Sects. 3.1 and 3.2). To this end, annual sums are computed for the Cabauw and Haarweg sites for the year 2005, using the fits of each individual year in the period investigated. The average of the four sums and the standard deviation are then compared with the average and standard deviation from all sites, using the respective model fits of the specific year of the observations (2005 in the case of Cabauw and Haarweg), again driven with *T<sub>a</sub>* and *R<sub>in</sub>* from Haarweg in 2005. Results are shown in Table 2. It can be seen that the absolute and relative variation in *GPP* and *R<sub>e</sub>* due to the interannual differences in ecophysiological characteristics are much smaller than the intersite variation (10–15% versus 35–37%),

**Table 3.** The mean annual sums of  $R_e$ ,  $GPP$ , and  $NEE$ , for the organic and mineral soil types for 2002 until 2005.

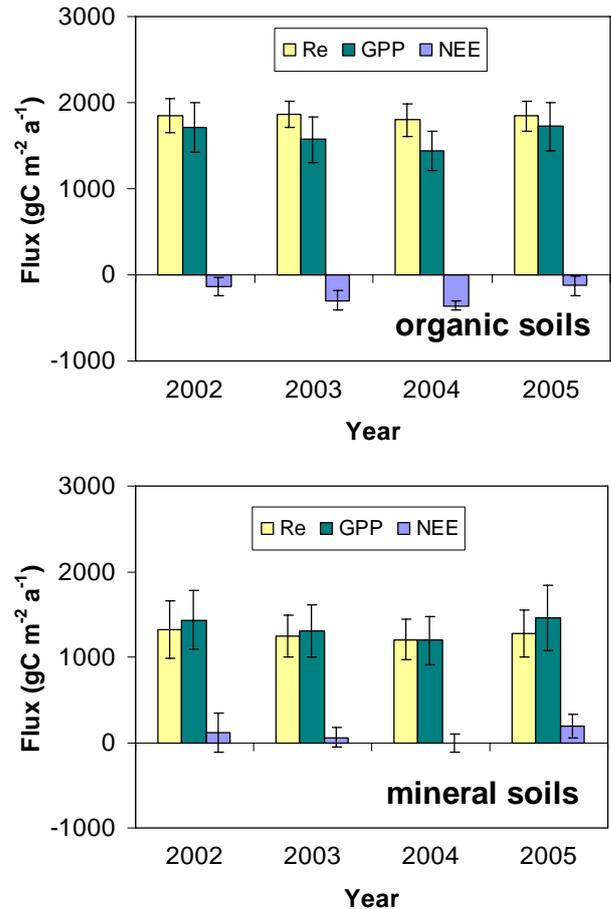
	Organic soils	Mineral soils
$R_e$ (gC m <sup>-2</sup> a <sup>-1</sup> )	1520±30	1260±50
$GPP$ (gC m <sup>-2</sup> a <sup>-1</sup> )	1300±100	1350±120
$NEE$ (gC m <sup>-2</sup> a <sup>-1</sup> )	-220±90	90±90

respectively). However, the standard deviation of the site-average is similar to the one of the period-average (207 versus 176–276 gC m<sup>-2</sup> a<sup>-1</sup>). Note that the CV of  $NEE$  given in the table shows a spurious behavior due to the small averages.

Variability in grassland emissions due to meteorological conditions and to ecophysiological conditions will not be independent in reality. Our analysis suggests that the interannual variability due to meteorological conditions may relatively small as compared to the variability due to ecophysiological differences, the difference being at least a factor of two for the sites investigate here. This illustrates the importance of long-term continuous observations that allow evaluation of the connection between meteorological conditions and ecophysiological characteristics. It also underlines the fact that interannual variability of CO<sub>2</sub> exchange cannot be evaluated using only climatic records with fixed ecophysiological conditions.

Depending on hydrology and management practices, grasslands on organic soils (e.g. peat) are often found to be sources for carbon dioxide (Nieveen et al., 1998; Nieveen et al., 2005; Lloyd, 2006; Veenendaal et al., 2007), while grasslands on mineral soils (for example, clay and sand) often show a net uptake for carbon dioxide (Gilmanov et al., 2007). Clearly it can be observed that the Fochteloërveen, Haastrecht, Oukoop and Stein sites follow this rule for organic soils and the Haarweg and Horstermeer sites for mineral soils. An exception appears to be the Cabauw site, which has a clay soil which sometimes reveals a net release of CO<sub>2</sub> (2002, 2003, 2004) and sometimes shows a net uptake (2005). Presumably, much of the variability of  $NEE$  of organic soils is caused by differences in management practices and hydrology of the areas.

To make a distinction between both soil types, the sums of the annual carbon fluxes are plotted separately for both soil types in Fig. 7 along with their standard deviations. From Fig. 7 we conclude that the annual standard deviations for all fluxes of the organic soils are much higher than those for the mineral soils. In our case this larger standard deviation is mainly caused by the Fochteloërveen bog site, which behaves quite differently from the other organic grassland sites. Second, we conclude that for both soil types the interannual differences in  $R_e$  are small in comparison to the interannual differences in  $GPP$  and as a consequence the interannual dif-

**Fig. 7.** The mean annual sums of  $R_e$ ,  $GPP$  and  $NEE$ , for the organic and mineral soil types during 2002 until 2005. Organic sites: Fochteloërveen, Oukoop, Stein, Haastrecht. Mineral sites: Haarweg, Cabauw, Lelystad, Horstermeer.

ferences in  $NEE$  are large as well. This also can be concluded from Table 3 where for both soil types the mean of the whole selected period has been given.

On average we conclude from Table 3 that the annual  $NEE$  amounts 90±90 gC m<sup>-2</sup> a<sup>-1</sup> for the mineral soils and -220±90 gC m<sup>-2</sup> a<sup>-1</sup> for the organic soils. As stated earlier, about 80% of the Dutch grasslands are on mineral soils and about 20% on organic soils. The weighed mean for the Dutch grasslands is 28±90 gC m<sup>-2</sup> a<sup>-1</sup>, indicating that, on average, the Dutch grasslands show a net uptake of CO<sub>2</sub>. Our results are in strong contrast with the emission factor used in the national inventory. Admittedly, our weighted average may be viewed as a rather simplistic upscaling method, but it puts the Dutch emission factor of 519 gC m<sup>-2</sup> a<sup>-1</sup> into perspective. The difference is due partly to the much smaller average release we found for the organic soils, in addition to the fact that uptake of grasslands on mineral soils was taken into account here. However, additional research is required to fully resolve the discrepancy.

Our results suggest that within small regions with relatively uniform climatic conditions the variability may be similar to the one observed at much larger scales with a large range of climatic conditions. At the European scale, Gilmanov et al. (2007) found the annual *GPP* to vary between 464 and 1881 gC m<sup>-2</sup> a<sup>-1</sup>, *R<sub>e</sub>* between 572 and 1636 gC m<sup>-2</sup> a<sup>-1</sup> and *NEE* between an uptake of 655 gC m<sup>-2</sup> a<sup>-1</sup> and a release of 164 gC m<sup>-2</sup> a<sup>-1</sup>. These numbers are based on gapfilled timeseries of observations. Our ranges in *GPP* and *R<sub>e</sub>* are similar to the one reported by Gilmanov et al. (2007): annual *GPP* varies between 391 and 2109 gC m<sup>-2</sup> a<sup>-1</sup>, and *R<sub>e</sub>* between 560 and 2047 gC m<sup>-2</sup> a<sup>-1</sup>. We find the *NEE* to vary between a net uptake of 307 gC m<sup>-2</sup> a<sup>-1</sup> and a release of 250 gC m<sup>-2</sup> a<sup>-1</sup>. Our results are based on ecosystem characteristics derived from on-site quality-controlled observations, extrapolated using response functions at the yearly timescale to the climatological conditions of one site. We feel that this method works satisfactorily for intersite-comparison and enables estimates of the relative contribution of climatological and ecophysiological conditions to the variability of CO<sub>2</sub> exchanges of grassland. Finally, comparison of the ranges in annual CO<sub>2</sub> exchange at the European and National (Dutch) scale, suggests that in order to properly assess regional GHG balances there is a need for detailed, regionally specific and spatially explicit CO<sub>2</sub> emission factors at the field scale. These are then the starting point to construct more complete assessments of the GHG balance. Such balances should include emissions of methane and nitrous oxide as well, and should take management factors and factors such as water table depth into account.

#### 4 Summary and conclusions

For eight Dutch grassland sites, CO<sub>2</sub> fluxes were determined using the Eddy Covariance technique during periods of at least 10 months per site. The measurement sites, four natural grasslands, two production grasslands and two meteorological stations within a rotational grassland region, are more or less distributed over the grassland areas in The Netherlands. The photosynthesis-light response analysis technique is used along with the respiration-temperature response technique to partition *NEE* among Gross Primary Production (*GPP*) and Ecosystem Respiration (*R<sub>e</sub>*) and to obtain the ecophysiological characteristics of the sites at the field scale. To assess annual sums of *NEE*, *R<sub>10</sub>*, *GPP* and their variability, calculations using the fitted response curves were then carried out for four years (2002–2005). Air temperature and solar radiation observed at the Haarweg meteorological station in the centre of The Netherlands were used as drivers of the response models. The main conclusions of this study are summarized as follows:

1. The annual *NEE* is estimated to be  $-65 \pm 85$  gC m<sup>-2</sup> a<sup>-1</sup>. A distinction can be made between the grass-

lands on mineral soils, with a mean net uptake of  $90 \pm 90$  gC m<sup>-2</sup> a<sup>-1</sup>, and those on organic soils with a mean net release of  $220 \pm 90$  gC m<sup>-2</sup> a<sup>-1</sup>. The mean *NEE* weighed with the fraction of grasslands on organic (20%) and mineral soils (80%) is  $28 \pm 90$  gC m<sup>-2</sup> a<sup>-1</sup>.

2. The main characteristics of the respiration-temperature response curves, *R<sub>10</sub>* and *E<sub>a</sub>*, of individual sites show an interannual variability which is much lower than the inter-site variability, with a variability coefficient of ~15% versus ~35%, respectively. The resulting corresponding variabilities in annual *R<sub>e</sub>* are similar. The variability due to interannual differences in weather conditions is much smaller, ~2%.
3. The intersite-variability of the light conversion factor,  $\alpha$ , is found to be about equal to the interannual variability of this parameter. It ranges from ~20 to ~60 %, depending on the air temperature. In contrast, the inter-site variability of *GPP*<sub>1000</sub> is clearly larger than the interannual variability. The standard deviation of *GPP*<sub>1000</sub> is ~10 to ~40% of the four-year averages and ~40 to ~60% of the means from all sites, again depending on the air temperature. The corresponding coefficients of variation for annual *GPP* derived from the fits are ~10 to 15% for the annual variability and ~37% for the intersite variability. Variability due to climatology is assessed to be ~8%.
4. The standard deviation of annual *NEE* due to interannual and intersite variability of ecophysiological differences is estimated to be 176–276 gC m<sup>-2</sup> a<sup>-1</sup> in both cases, as compared to 85 gC m<sup>-2</sup> a<sup>-1</sup> for variability due to meteorological conditions. The latter number does not account for possible correlations between ecophysiological and meteorological factors. This, along with the differences between the two sources of variability underline the need for long-term flux observations.
5. Our variability estimates are similar to those on a much larger, European scale. This suggests that in order to properly assess regional GHG balances there is a need for detailed, regionally specific and spatially explicit CO<sub>2</sub> emission factors at the field scale.

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