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# Simultaneous measurements of CO<sub>2</sub> and water exchanges over three agroecosystems in South-West France

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**Abstract.** During the last few decades, many studies have been performed to determine water and carbon budgets of broadleaf and deciduous forests, crops and grasslands. However, since most measurements have been made in different regions and at different periods, it is difficult to compare the results directly. In order to evaluate accurately the respective contribution of various agroecosystems to global water and carbon exchanges, it is necessary to compare data obtained in similar climatic and weather conditions. To address this question, we present the results from simultaneous measurements carried out during one year over three typical agroecosystems of the Les Landes region in South-West France: an agricultural field with maize from 29 May to 18 October, a young (5 year-old) pine forest and a mature (37 year-old) pine forest. All measurements were collected as part of the Regional Experiment component of the CarboEurope-IP project. During most of the year, the agricultural field without vegetation is a source of CO<sub>2</sub>, but from late June to early September the maize crop becomes a stronger carbon sink than the forests. Over the whole measurement period the three agroecosystems behave as CO<sub>2</sub> sinks with carbon storage of about 335, 210 and 160 g C m<sup>-2</sup> for the young forest, the mature forest and the agricultural field, respectively. We investigated the influence of climatic conditions on Gross Primary Production (GPP) of the three ecosystems and observed a predominant role of vapour pressure deficit (VPD) for forests and of photosynthetic photon flux density ( $F_{PP}$ ) for maize. Daily Water Use Efficiencies (WUE) of the three ecosystems were evaluated and expressed as functions of the mean daily vapour pressure deficit (VPD). Similar trends were observed for the two forests, which suggests that for a given species WUE is independent of stand age. The WUE of the maize crop at maturity was also found to

depend upon VPD, but it is about twice as large as for the forests, owing to the physiological advantages of C<sub>4</sub> species.

## 1 Introduction

Global warming and the atmospheric increase of carbon dioxide, related to human activities, call for a better understanding of the terrestrial carbon cycle. In this context, it is necessary to quantify the respective contribution of the various ecosystems composing the terrestrial biosphere to global carbon exchanges. Their role of source or sink of CO<sub>2</sub> depends on species physiology and climatic conditions. In particular, the capacity of ecosystems to stock carbon has been shown to depend strongly on water availability. Yet, for the next 100 years, models predict variations in rainfall with an increase or a decrease according to regions (IPPC, 2001). In southern Europe, models predict a decrease of annual rainfall by about 20% (IPPC, 2007). Therefore, a joint analysis of water and carbon fluxes is a necessity.

In order to facilitate the study of carbon dioxide and water vapour exchanges between the atmosphere and the biosphere, the eddy-covariance method has been developed and extensively used in programmes such as Euroflux (Aubinet et al., 2000) and FLUXNET (Baldocchi et al., 2001). During the last decades, several studies have been performed over forests (Berbigier et al., 2001; Kowalski et al., 2003, 2004; Misson et al., 2007; Jarosz et al., 2008), crops (Suyker et al., 2004; Verma et al., 2005; Moureaux et al., 2006) and grasslands (Xu and Baldocchi, 2004; Ma et al., 2007; Kjelgaard et al., 2008). However, since most measurements have been made in different regions and at different periods, it is difficult to compare the results directly. To evaluate the specific role of each ecosystem in the biosphere-atmosphere carbon exchanges, it is necessary to analyse data obtained in similar climatic and weather conditions, i.e. at a regional scale during the same period.



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In the present study, we report simultaneous measurements of water vapour (H<sub>2</sub>O) and carbon dioxide (CO<sub>2</sub>) fluxes performed with the eddy-covariance method from March 2007 to February 2008 above three ecosystems of the Les Landes region in South-West France: an agricultural field with a maize crop from late May to mid-October, irrigated in summer, a 5 year-old pine forest and a 37 year-old pine forest. This measurement campaign was part of the Regional Experiment component of CarboEurope-IP (Dolman et al., 2006). The objectives of this paper are: (i) to analyse for each ecosystem the effect of environmental conditions on the components of Net Ecosystem Exchange (NEE), i.e. Gross Primary Production (GPP) and ecosystem respiration ( $R_e$ ), (ii) to characterize and compare the Water Use Efficiency (WUE) of the forests and the maize crop and (iii) to determine the carbon budgets of the three ecosystems, in similar climatic and weather conditions, over the whole measuring period.

## 2 Material and methods

### 2.1 Site characteristics

#### 2.1.1 “Le Bray” site

The experimental site of Le Bray is located in the Les Landes forest about 20 km South-West of Bordeaux (latitude 44°43′33.24″ N, longitude 0°46′33.72″ W, altitude 62 m) in France. A 40 m high instrumented tower is set up in the middle of a maritime pine stand (*Pinus pinaster* Ait.) planted in 1970 and covering about 16 ha. In 2007 the canopy crown extended between 14 and 22 m above the soil surface and the stand density was about 410 trees ha<sup>-1</sup>. The understorey vegetation consists essentially of grasses (*Molinia coerulea* L.) in wet areas, with sparse ferns (*Pteridium aquilinum* L.) in mesophyl areas. The soil is a sandy and hydromorphic podzol, with dark organic matter in the first 0.6 m. It is covered by a litter formed by dead needles, dead grass, dead branches and decayed organic matter. The water table level usually reaches the soil surface in winter and drops to a depth between 1.2 and 2 m in summer.

#### 2.1.2 “Bilos” site

The experimental site of Bilos is also located in the Les Landes forest, at about 50 km South-West of Bordeaux (latitude 44°31′18.15″ N, longitude 0°53′45.54″ W, altitude 50 m). Two 6 m high instrumented towers (one for the meteorological measurements and one for the turbulence) are set up in the middle of a young stand of maritime pine planted in 2002 and covering about 30 ha. In 2007, the height of the pines was about 2.5 m. The understorey is made of different species of small plants, heather *Calluna Vulgaris* L., commun-furge *Ulex Europaeus* L., pokeberry *Phytolaca Americana* L. and purple moor-grass *Molinia coerulea* L. Moench. The soil is

a sandy and hydromorphic podzol, with dark organic matter in the first 0.6 m. It is covered by a litter formed by dead needles, dead grass, dead branches and decayed organic matter. The water table level reaches the soil surface during most winters and drops to a depth of 2.5 m in summer.

#### 2.1.3 “La Cape Sud” site

The experimental site of La Cape Sud is located at about 60 km South of Bordeaux (latitude 44°24′24.69″ N, longitude 0°38′36.55″ W, altitude 52 m). In 2007, a 6 m high instrumented mast was set up in the middle of a 2 ha field sown with maize (*Zea mays* L.) on 26 April 2007. The maize emerged on 29 May 2007 and stopped growing on 11 July approximately; senescence started around 1 September 2007. This field was harvested between the 11 October and 18 October 2007. The plot was regularly irrigated from June to August by two ramps, with a 400 m radius in the west direction and a 350 m radius in the east direction. The soil is sandy with a dark organic matter layer in the first 0.4 m.

### 2.2 Eddy-covariance and meteorological measurements

At the three sites the turbulent fluxes are measured by an EC system (at 41 m above ground at Le Bray, and 6.4 m at the other two sites). The EC systems consist in a 3-D sonic anemometer (a Solent R2 – Gill Instruments, Lymington, Hampshire, UK – at Le Bray and a Young 81000V – R. M. Young Company, Traverse City, Michigan, USA – at Bilos and La Cape Sud) coupled with CO<sub>2</sub>/H<sub>2</sub>O InfraRed Gas Analyzers (an open-path LI-7500 at Le Bray and Bilos and a close-path LI-7000 at La Cape Sud, all from LICOR, Lincoln, NE, USA). Instantaneous measurements of the three components of wind velocity, temperature ( $T$ ) and the molar fractions of H<sub>2</sub>O and CO<sub>2</sub> are collected and stored on a PC using Tourbillon Software (INRA Ephyse, France), at 20.8 Hz at Le Bray and 20 Hz at the other two sites. Turbulent scalar eddy fluxes are calculated every half hour as the covariance between the vertical wind speed and the scalar variable (CO<sub>2</sub>, H<sub>2</sub>O,  $T$ ).

At each site net radiation ( $R_n$ ) is measured with a NrLite Pyrriadiometer (Kipp & Zonnen, Delft, The Netherlands) and the incident short-wave radiation is measured with a CE180 pyranometer (Cimel Electronique, Paris, France). The incident and diffuse photosynthetic photon flux density ( $F_{PP}$ ) are measured above each canopy using either a sunshine sensor BF2 (Le Bray and Bilos) or BF3 (La Cape Sud, all from Delta-T Devices, Cambridge, UK). At Le Bray site an extra pyranometer is used to measure the reflected short-wave radiation, and the incident and reflected long-wave radiation fluxes are measured using a CG2 pyrgeometer (Kipp & Zonnen).

Mean wind speed and direction are measured with a Young 5103 wind vane anemometer (R. M. Young Company, Traverse City, Michigan, USA) at Le Bray and La

Cape Sud. At Bilos, mean wind speed is measured by a CE150 anemometer (Cimel Electronique, Paris, France) and wind direction with a WP200 wind vane (Campbell Scientific, Logan Utah, USA). At all three sites air temperature and relative humidity are measured with a HMP45 (Vaisala, Helsinki, Finland). All these measurements are performed at the same height as the flux measurements. Atmospheric pressure was measured at 2 m above ground at Le Bray site, using a PTB101B barometric pressure transmitter (Vaisala, Helsinki, Finland).

Rain gauges ARG100 (Campbell Scientific, Logan, USA) were used to measure rainfall. At Le Bray it was measured at a height of 24 m on a nearby tower, just above the top of the trees. At Bilos it was also measured on a nearby tower, at a height of 3 m, just above the top of the trees. At La Cape Sud two rain gauges are used: one was set up at 200 m from the mast in a non-irrigated zone in order to measure rainfall and the other one measured the sum of irrigation and rainfall, near the mast at a height of 4 m, above the maize crop.

Soil heat flux ( $G$ ) was measured at Le Bray site using five flux plates (Campbell Scientific, Logan Utah, USA) and corrected from heat storage in the top soil layer using a two-step version of the null-alignment method (Ogée et al., 2001). For this, soil temperature, water content and bulk density measurements were taken between the soil surface and 1 m depth. Four soil temperature profiles were set up at depths 0.01, 0.02, 0.04, 0.08, 0.16, 0.32, 0.64 and 1 m using 32 homemade thermocouples. The soil water content (SWC) was measured at 0.05, 0.23, 0.34 and 0.8 m depth using Campbell CS615 probes (Campbell Scientific, Logan Utah, USA) at three different locations. A similar protocol was used at the Bilos site, with three HFP01SC soil heat flux plates (Hukseflux thermal sensors, Delft, The Netherlands). Two soil temperature sensors were buried at depths of 0.05 and 0.1 m and four temperature profiles were set up at 0.01, 0.02, 0.04, 0.08, 0.16, 0.32, 0.64 and 1 m using another set of 32 homemade thermocouples. SWC was measured at 0.15, 0.30, 0.45, 0.60 and 0.80 m using CS615 probes at the same four locations. At La Cape Sud one temperature profile was set up at depths 0.01, 0.05, 0.1, 0.2, 0.3, 0.4 and 1 m using 7 homemade thermocouples. SWC was measured at 0.1, 0.2, 0.3 and 0.4 m using 4 CS615 probes. A Delta-T Teta probe (Delta-T Devices, Cambridge, UK) was also used to measure mean SWC over the first 5 cm. At all sites soil bulk density was measured gravimetrically from samples collected at various depths and several locations in the vicinity of the other soil measurements.

All microclimatic data were sampled every 10 s on Campbell data loggers (CR10X, CR21X and CR23X at Le Bray, CR1000 and CR23X at Bilos, CR23X and CR21X at La Cape Sud) and averaged every half hour.

## 2.3 Processing methods

### 2.3.1 Eddy-covariance fluxes

All turbulent fluxes were computed and corrected over 30 min periods using the EdiRe software (Moncrieff et al., 1997) as recommended during the workshop “Standardization of Flux Diagnostics and Analysis Guidelines” (Corvalis, Oregon 27–30 August 2002). All fluxes were computed by block averaging with linear detrending applied only on scalar time series. Coordinate axes were rotated using a planar fit at Le Bray (tall forest) and using a 2-D rotation method at La Cape Sud and Bilos (maize and short forest, respectively). At all sites the mean horizontal velocity was aligned with the mean wind direction. High frequency losses were corrected using the approach of Massman (2000) at La Cape Sud (where a close-path system was used) and the approach of Moore (1986) at the other two sites. Where open-path systems were used (Le Bray and Bilos), water vapour and carbon dioxide fluxes were corrected for the effects of density fluctuations (Webb et al., 1980) and instrument surface heat exchanges (Burba et al., 2008).

The quality criteria were defined following the “QA/QC methodology for Eddy-covariance measurements” (Ameriflux, 1st QA/QC workshop, Thurnau, 2002). Tests (spikes, sampling errors, resolutions, physical limits) were performed on all raw datasets using the methodology of Vickers and Mahrt (1997). Algorithms from Vickers and Mahrt (1997) and Foken and Wichura (1996) were used for steady state tests. For the turbulence characteristics tests, we used the algorithm of Kaimal and Finnigan (1994). Half-hourly flux values that were missing or did not meet the quality criteria were gap-filled. The detailed method can be found in Berbigier et al. (2001).

### 2.3.2 Partitioning CO<sub>2</sub> flux

Net Ecosystem Exchange (NEE) was partitioned between Gross Primary Production (GPP) and Ecosystem Respiration ( $R_e$ ). According to Kowalski et al. (2003, 2004), daytime NEE ( $NEE_d$ ) can be expressed as a curvilinear function of the photosynthetic photon flux density ( $F_{PP}$ ):

$$NEE_d = \frac{a_1 F_{PP}}{a_2 + F_{PP}} - \overline{R_{ed}} \quad (1)$$

where  $\overline{R_{ed}}$  is the mean daytime ecosystem respiration,  $a_1$  is the maximum photosynthetic uptake rate at light saturation and  $a_2$  is the light level corresponding to half the maximum uptake, at the time scale of the non-linear regression of  $NEE_d$  vs.  $F_{PP}$ . Those parameters were determined at daily scale. However, in this paper, GPP was not modelled as a function of  $a_1$ ,  $a_2$  and  $F_{PP}$ , but calculated half hourly as the difference between experimental half hourly values of  $NEE_d$  and the mean daytime ecosystem respiration  $\overline{R_{ed}}$ .

Provided that turbulent mixing is sufficient ( $u_* > 0.2 \text{ m s}^{-1}$ ), measurements of nighttime NEE ( $NEE_n$ ) directly

give nighttime respiration ( $R_{en}$ ) at half hourly scale. Data for  $u_* > 0.2 \text{ m s}^{-1}$  were fitted to an exponential  $Q_{10}$  function of soil temperature as:

$$R_{en} = R_{en,15} Q_{10}^{(T_s-15)/10} \quad (2)$$

where  $R_{en,15}$  is the nighttime respiration flux at a reference temperature ( $T_s=15^\circ\text{C}$ ) and  $Q_{10}$  is the sensitivity to temperature. Equation (2) was then used to estimate  $R_{en}$  in low turbulence conditions.

For each night of the measurement campaign, the mean nighttime ecosystem respiration ( $\overline{R_{en}}$ ) was calculated combining experimental (for  $u_* > 0.2 \text{ m s}^{-1}$ ) and modelled (for  $u_* < 0.2 \text{ m s}^{-1}$ ) half-hourly values of  $R_{en}$ .

### 2.3.3 Estimating stomatal conductance

The stomatal conductance for CO<sub>2</sub> ( $g_s$ ) can be deduced from the stomatal conductance for water vapour, the latter being inferred from the water vapour flux measurements by inverting the Penman-Monteith equation (Monteith, 1981):

$$g_s = \frac{D_{\text{CO}_2}}{D_{\text{H}_2\text{O}}} \frac{\frac{E}{\sigma_w}}{1 + \frac{E}{\sigma_w} (R_a + R_b) \left( \frac{\beta s}{\gamma} - 1 \right)} \quad (3)$$

where  $D_{\text{CO}_2}$  and  $D_{\text{H}_2\text{O}}$  ( $\text{m}^2 \text{ s}^{-1}$ ) are the molecular diffusivity for CO<sub>2</sub> and water vapour, respectively ( $D_{\text{CO}_2}/D_{\text{H}_2\text{O}} \approx 0,62$ ),  $E$  is the water vapour flux ( $\text{kg m}^{-2} \text{ s}^{-1}$ ),  $\sigma_w$  the water vapour density saturation deficit ( $\text{kg m}^{-3}$ ),  $\beta$  the Bowen ratio,  $s$  the slope of the saturation curve ( $\text{K}^{-1}$ ),  $\gamma$  the psychrometric constant ( $\text{K}^{-1}$ ) and  $R_a$  and  $R_b$  the aerodynamic and boundary layer resistances ( $\text{s m}^{-1}$ ), respectively.

However, this estimation of  $g_s$  requires that  $E$  represents only plant transpiration, without including evaporation of liquid water (rain, irrigation, dew) which may be present at the vegetation surface. Therefore, it is not valid after irrigation and rainfall events or in conditions of high air relative humidity.

## 3 Results and discussion

### 3.1 Annual time series of NEE

Figure 1a and b shows the annual evolutions of  $F_{PP}$  and the rainfall measured at Le Bray, which are also representative of the other two sites. The variations of half hourly NEE at each site are represented in Fig. 1c, d and e. Figure 1f shows the variation in maize height from 29 May to 18 October. The beginning of maize senescence and the harvest period are also indicated.

NEE is of the same order for the two forests (Fig. 1c and d), with a maximum in late June (approximately  $30 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) and a minimum in December. These annual variations are related to those of  $F_{PP}$  (Fig. 1a), since solar radiation is the dominant environmental factor controlling

CO<sub>2</sub> exchange between the atmosphere and the biosphere through its effect on both stomatal aperture and photosynthesis (Steduto and Hsiao, 1998a; Falge et al., 2002; Suyker et al., 2004).

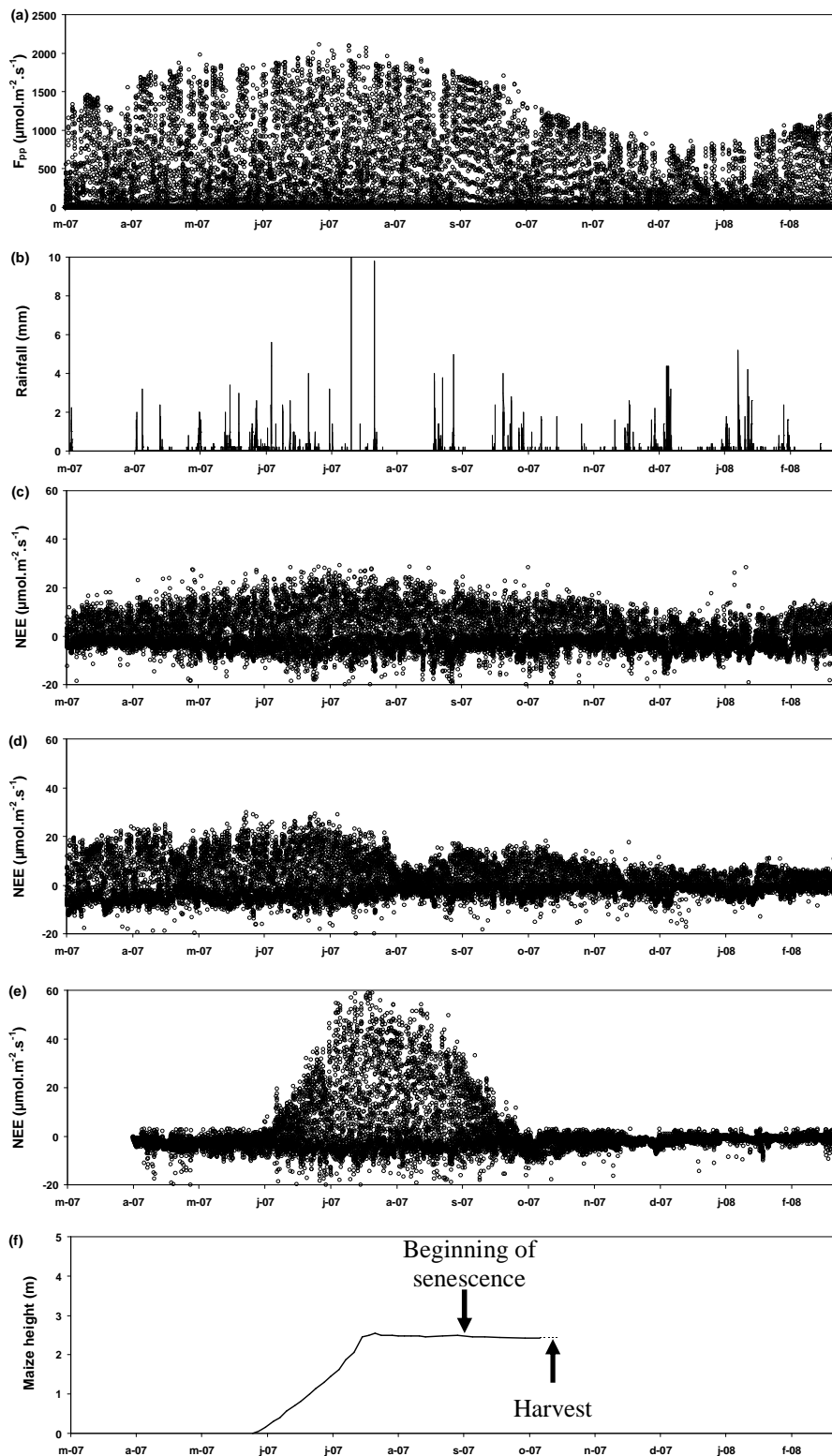
However, some differences in the annual evolution of NEE appear between the two forests. First of all, NEE is about 50% higher for the young forest (Bilos) than for the mature one (Le Bray) from early March to mid-April 2007, which may be due to the difference between the understoreys of the two stands (Sects. 2.1.1 and 2.1.2). Secondly, a large difference appears during the first three weeks of August, a quite long period without rainfall (Fig. 1b), when the NEE of Bilos strongly decreases (Fig. 1d) whereas the NEE of Le Bray remains stable (Fig. 1c). This point is detailed in the next section.

Regarding the agricultural field, the dynamics of NEE is essentially controlled by the phenology of the maize (Fig. 1e). The site is a source of CO<sub>2</sub> during the period with bare soil (before 29 May), but also during the early growth of the maize (from 29 May to 8 June), as long as photosynthesis is not large enough to compensate for ecosystem respiration. NEE increases during the growth of maize, up to a maximum of about  $60 \mu\text{mol m}^{-2} \text{ s}^{-1}$  at the beginning of the maturity phase, around the 10 July. It remains at this maximum during a very short period then decreases from mid-July along with the decrease in solar radiation (Fig. 1a). The senescence, which starts around the 1 September, accelerates the decrease of NEE. The field becomes again a source of CO<sub>2</sub> from late September, although maize is harvested only after mid-October.

### 3.2 Factors affecting GPP

This section notably concerns the period from 24 July 2007 (DOY 205) to 20 August 2007 (DOY 232), marked by the absence of rainfall, but during which the maize crop was irrigated. Figure 2 presents time series of  $F_{PP}$ , VPD and GPP for each site.

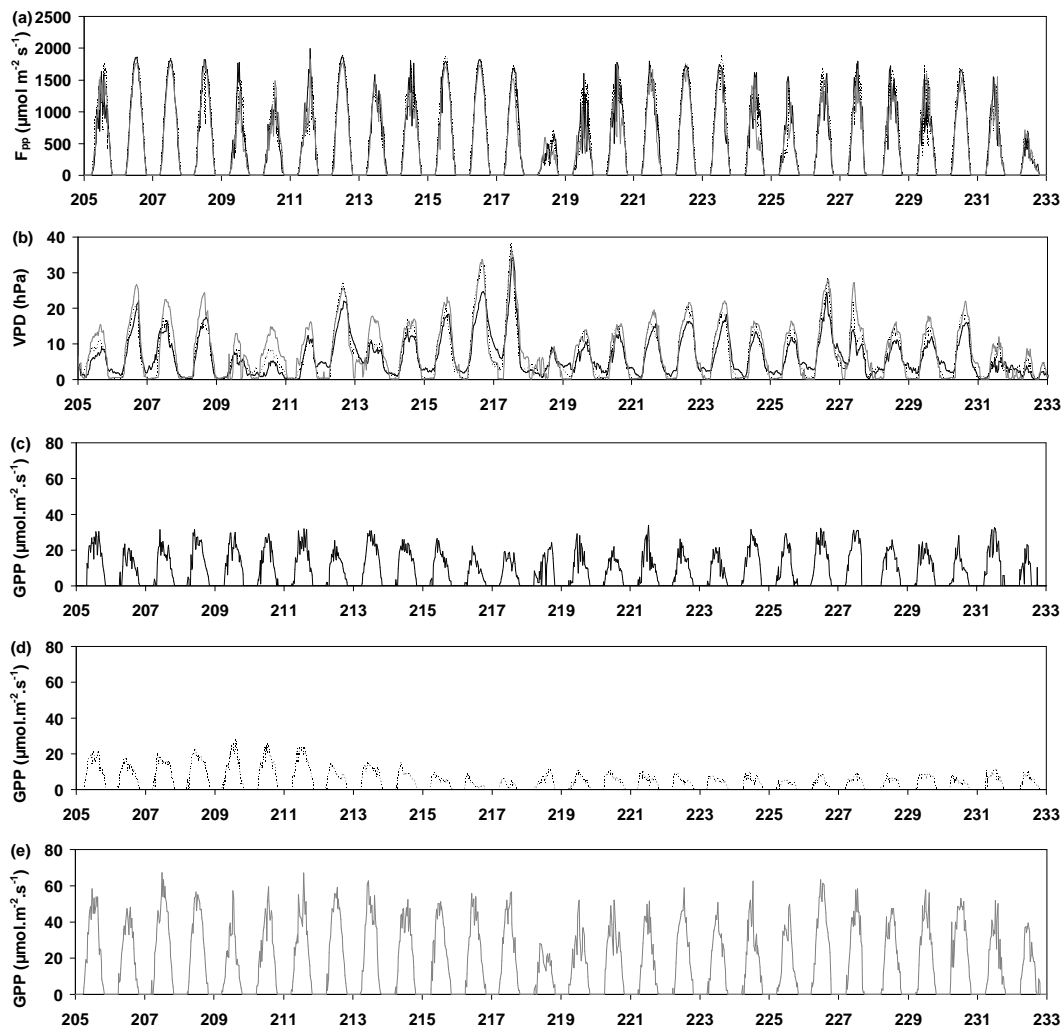
From DOY 205 to 211, GPP is of the same order for the two forests, around  $20 \mu\text{mol m}^{-2} \text{ s}^{-1}$  in the middle of the day (Fig. 2c and d). From DOY 212 to 232, and especially from DOY 215 onwards, GPP of Bilos decreases to less than  $10 \mu\text{mol m}^{-2} \text{ s}^{-1}$  at midday whereas GPP of Le Bray remains at the same level as before. As indicated in Table 1, accumulated GPP at Bilos is 47% lower over the period from DOY 205 to 232 than over the previous well-watered period of 28 days, while at Le Bray it is only 11% lower. This strong decrease in GPP of the young forest is related to the soil water content (SWC) of the Bilos site. On both forest sites, SWC decreases in August with the absence of rainfall. However SWC is always larger at Le Bray than at Bilos. On DOY 205, values of SWC at 0.8 m depth are 28% and 13% for Le Bray and Bilos, respectively. From DOY 205 to 232, SWC of Bilos decreases to 9%, before increasing again with the rainfall of DOY 233. On DOY 212, when we observe a decrease



**Fig. 1.** Half-hourly values of photosynthetic photon flux density ( $F_{PP}$ ) (a) and rainfall (b) measured at the Le Bray site, and Net Ecosystem Exchange (NEE) at Le Bray (c), Bilos (d) and La Cape Sud (e), for which we also represent the time change in maize height (f). Note that measurements at La Cape Sud only began at the end of March 2007.

**Table 1.** Total rainfall (mm) and accumulated gross primary production (g C m<sup>-2</sup>) at Le Bray, Bilos and La Cape Sud during well-watered (from DOY 177 to DOY 204) and no rainfall (from DOY 205 to DOY 232) periods. For La Cape Sud, rainfall includes irrigation.

	Rainfall Le Bray	Rainfall Bilos	Rainfall La Cape Sud	GPP Le Bray	GPP Bilos	GPP La Cape Sud
DOY 177 to 204	31.0	29.6	163.6	268	249	477
DOY 205 to 232	0	0	122.4	239	131	482



**Fig. 2.** Time series of photosynthetic photon flux density (a), vapour pressure deficit (b) and gross primary production (c to e) for each site from 24 July 2007 (DOY 205) to 20 August 2007 (DOY 232). Note that in (a) and (b), the black lines are for Le Bray, the dotted lines for Bilos and the grey lines for La Cape Sud, as in panels (c) to (e).

in GPP of the Bilos stand, the value of SWC is 12%. It is well known that a decrease in SWC, inducing a lower maximum sustainable water flux, provokes stomatal closure in order to limit water losses (Williams et al., 2001). The results from the Bilos site suggest that, for maritime pine forests, this phenomenon appears at a threshold value of 12% for SWC at 0.8 m depth. As SWC of the Le Bray site does not drop be-

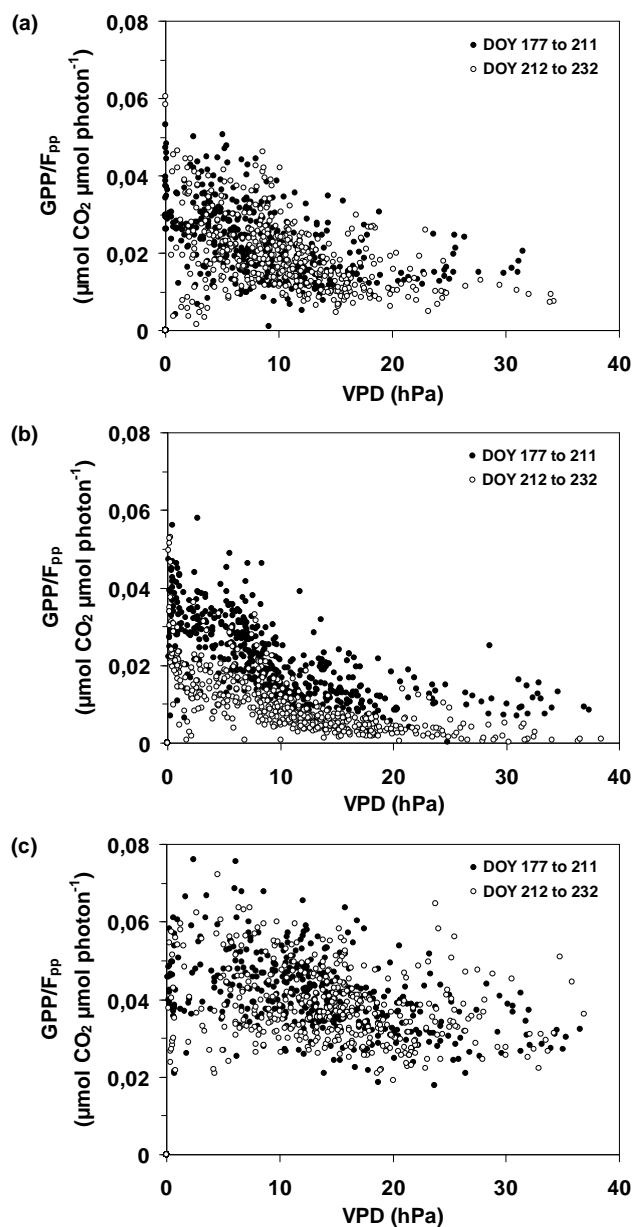
low this threshold value during the dry period (its minimum value is 13% on DOY 232), this would explain why we do not observe water stress effects on the GPP of this stand.

Beside this difference between Le Bray and Bilos, Fig. 2 calls for several comments concerning the day-to-day variability of GPP for the three sites. For the maize crop (Fig. 2e) this variability seems to be positively correlated with the one

of  $F_{PP}$ , as can be seen in the period from DOY 217 to 222, especially on DOY 218. However, no such correlation between GPP and  $F_{PP}$  is visible for the two forests (Fig. 2c and d). At the opposite, GPP seems to be negatively correlated with VPD for the two forest sites (see the period from DOY 211 to 217 in Fig. 2c and d) but not for the maize crop (Fig. 2e). Since  $F_{PP}$  and VPD are themselves often positively correlated, it is difficult to analyse their respective influence upon GPP merely from the time series of Fig. 2. For this purpose, we plotted for each site the ratio  $GPP/F_{PP}$  vs. VPD in Fig. 3. This figure shows the data from DOY 205 to 232, as in Fig. 2, and also, for comparison, those from the previous well-watered period of 28 days. However, since we observed in Fig. 2 that the Bilos site was still not affected by water stress during the first week (DOY 205 to 211) of the dry period, those data are regrouped with those of the well-watered period in Fig. 3.

For the forest of Le Bray (Fig. 3a) and the maize crop (Fig. 3c), no difference is visible between the two data sets. However, for the forest of Bilos (Fig. 3b), the effect of soil water deficit on the second period is obvious, with a much lower value of the ratio  $GPP/F_{PP}$  whatever the values of VPD. Apart from this difference of magnitude, the variation of  $GPP/F_{PP}$  with VPD is similar for the two data sets. The general form of this variation is also the same for the forest of Le Bray and the maize crop, with a sort of a plateau for VPD lower than 10 hPa and a decrease of  $GPP/F_{PP}$  at higher values of VPD. However, there are quantitative differences between the three sites, as for Bilos between the two periods. The value of the plateau is maximal for the maize crop (around  $0.045 \mu\text{mol CO}_2 \mu\text{mol photon}^{-1}$ ) and the decrease of  $GPP/F_{PP}$  with increasing VPD is also less marked than for the forest sites. The latter fact confirms that the influence of VPD upon GPP of the maize crop is weak, as suggested by Fig. 2, although it really exists. For Le Bray, as well as for Bilos during the period without water stress, the value of the plateau is about  $0.03 \mu\text{mol CO}_2 \mu\text{mol photon}^{-1}$  and, for the highest VPD,  $GPP/F_{PP}$  drops to less than  $0.02 \mu\text{mol CO}_2 \mu\text{mol photon}^{-1}$ , which is more than twice as low as for the maize crop. The pronounced effect of VPD on the GPP of these two forests is in agreement with the conclusions of Williams et al. (2001), who stated that a high atmospheric demand for water exceeding soil-plant hydraulic system provokes stomatal closure, inducing a decrease in GPP.

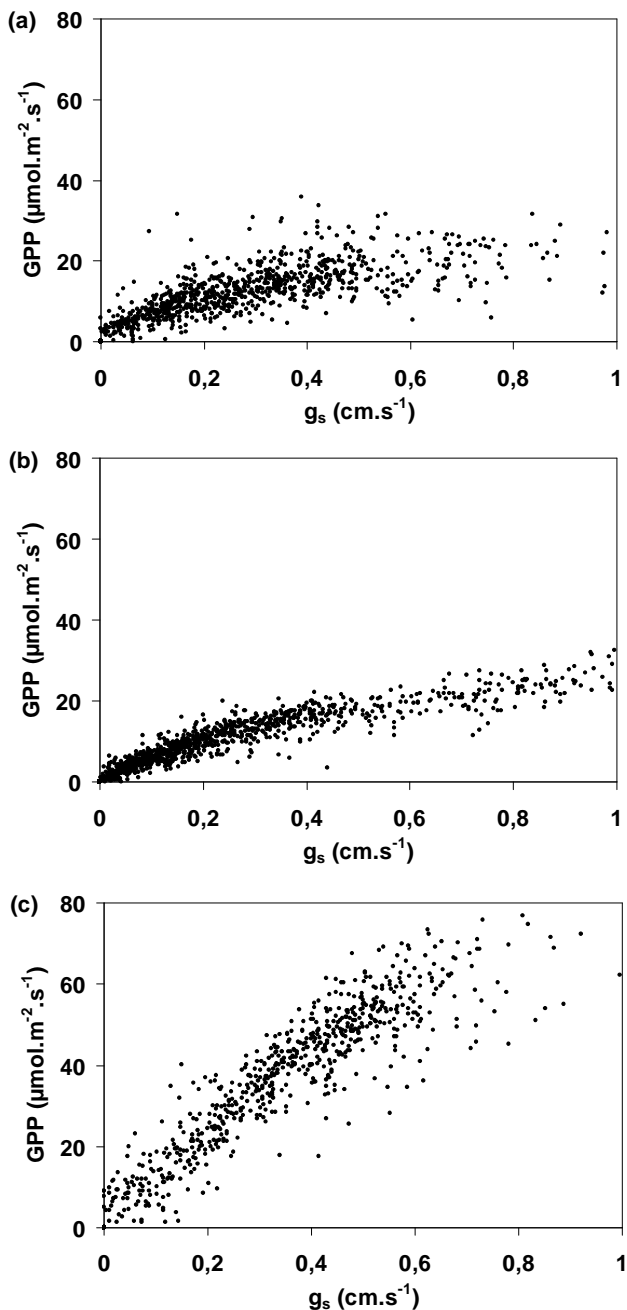
The low dependence of  $GPP/F_{PP}$  to VPD for the irrigated maize crop has for consequence that the variations of its GPP are essentially controlled by  $F_{PP}$ . This explains the correlation observed between those two variables in Fig. 2. Figure 3a and b also allows us to understand why this correlation was not visible for the two forest sites. In this case, the increase of GPP with  $F_{PP}$  is compensated by the decrease of  $GPP/F_{PP}$  due to the simultaneous increase in VPD. If the effects of  $F_{PP}$  and VPD cancel each other out, no correlation will be observed neither positive between GPP and  $F_{PP}$ , nor negative between GPP and VPD. This is generally the case



**Fig. 3.** Gross primary production (GPP) normalized by photosynthetic photon flux density ( $F_{PP}$ ) vs. vapour pressure deficit (VPD) for Le Bray (a), Bilos (b) and La Cape Sud (c). The two data sets correspond to (i) DOY 177 to 204 (well-watered period) and DOY 205 to 211 (beginning of the dry period, without still no effect of water stress at the Bilos site); (ii) DOY 212 to 232 (second part of the dry period, when water stress effects appear at the Bilos site).

in Fig. 2 because increases of  $F_{PP}$  and VPD are most often correlated (see the period from DOY 218 to 232). However, from DOY 211 to 217, the large day-to-day variability of VPD, whereas  $F_{PP}$  remains fairly stable, allows us to observe a significant negative correlation between GPP of the two forests and VPD.





**Fig. 4.** Gross primary production (GPP) vs. stomatal conductance ( $g_s$ ) for Le Bray (a) and Bilos (b) from June to September 2007 and La Cape Sud during the maturity phase of the maize, from 11 July to 1 September (c).

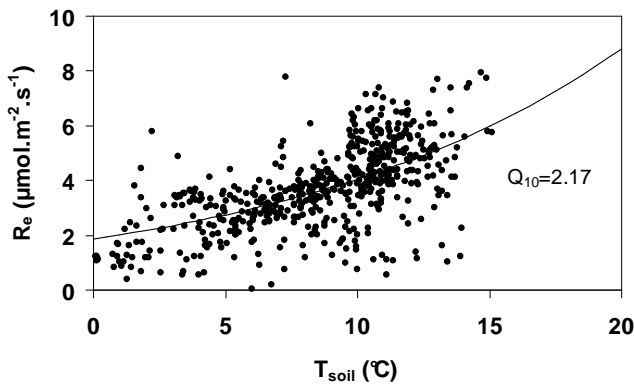
### 3.3 Comparison of carbon uptake potential between irrigated maize crop and pine forests

At its maximum physiological activity, when there is no limiting factor such as low radiation, GPP of the maize crop is more than twice as large as those of the two forests (see Fig. 2 at the beginning of the period). These results are in agree-

ment with those from Verma et al. (2005) who observed that peak CO<sub>2</sub> uptake for maize was about two to three times as large as the values reported for temperate forests. According to Falge et al. (2002), this pattern is common: maximum CO<sub>2</sub> uptake is achieved by crops (especially C<sub>4</sub> plants), then temperate deciduous forests, temperate coniferous forests and boreal coniferous forests; tundra ecosystems have the minimum uptake. However, since those studies were performed in different countries, these differences may also be partly due to differences in climate. This is not the case for the present analysis, since climatic and weather conditions are identical for the three sites. As the sites also have similar soils, only species properties can therefore explain the observed differences in carbon uptake. It also has to be remembered that, due to irrigation, the maize crop is not submitted to water stress. According to Verma et al. (2005), the absence of irrigation can induce a decrease in GPP by about 12.5% for a maize crop. However, throughout the measuring period, water stress only affects the young forest during three weeks in August, so that both forests are most of the time at their maximum carbon uptake potential, as is the maize crop.

The first explanation of the difference in GPP between maize and pine forests is related to canopy morphology. When maize is fully developed it has a much larger Leaf Area Index than maritime pine (LAI=5.1, 2.5 and 1.9 m<sup>2</sup> m<sup>-2</sup>, for maize, mature and young forests, respectively), and recent studies have shown a high positive correlation between GPP and LAI (Steduto and Hsiao, 1998a, b; Suyker et al., 2004; Xu and Baldocchi, 2004). However, the role of LAI pointed out by these authors is quantitatively too weak to explain a value of GPP twice as large for the maize crop as for the forests.

We present in Fig. 4 the relationship between GPP and the stomatal conductance ( $g_s$ ) for each ecosystem. For the reasons explained in Sect. 2.3.3, data following irrigation and rainfall events by less than one day and data corresponding to air relative humidity higher than 60% were not included in this figure. At a given value of stomatal conductance, GPP appears lower for the forests (Fig. 4a and b) than for the maize (Fig. 4c). This is due to physiological differences between C<sub>3</sub> (pines) and C<sub>4</sub> (maize) species. CO<sub>2</sub> fixation for C<sub>3</sub> species is catalysed by ribulose biphosphate carboxylase (RuBPCase). However, this enzyme is equally able to fix O<sub>2</sub>, so that CO<sub>2</sub> and O<sub>2</sub> are in competition. For C<sub>4</sub> species, CO<sub>2</sub> is first fixed by phosphoenolpyruvic carboxylase (PEPCase) in cytoplasm of mesophyll cells, before integrating Benson-Calvin cycle via RuBPCase in the bundle-sheath cells (Romberger et al., 1993). Therefore, there is no competition between CO<sub>2</sub> and O<sub>2</sub>. Furthermore, PEPCase have a better affinity to CO<sub>2</sub> than RuBPCase. Moreover, C<sub>3</sub> species undergo two photosynthetic limitations under high light intensity, the maximum speed of carboxylation and the maximum speed of electron transport (Farquhar et al., 1980). This is why photosynthetic assimilation of C<sub>3</sub> species is a curvilinear function of stomatal conductance ( $g_s$ ), while it is



**Fig. 5.** Relationship between half-hourly values of ecosystem respiration ( $R_e$ ) and soil temperature ( $T_{\text{soil}}$ ) at La Cape Sud after maize harvest. The dark line represents the  $Q_{10}$  function. Only data with  $u_* > 0.2 \text{ m s}^{-1}$  are represented and used for the regression.

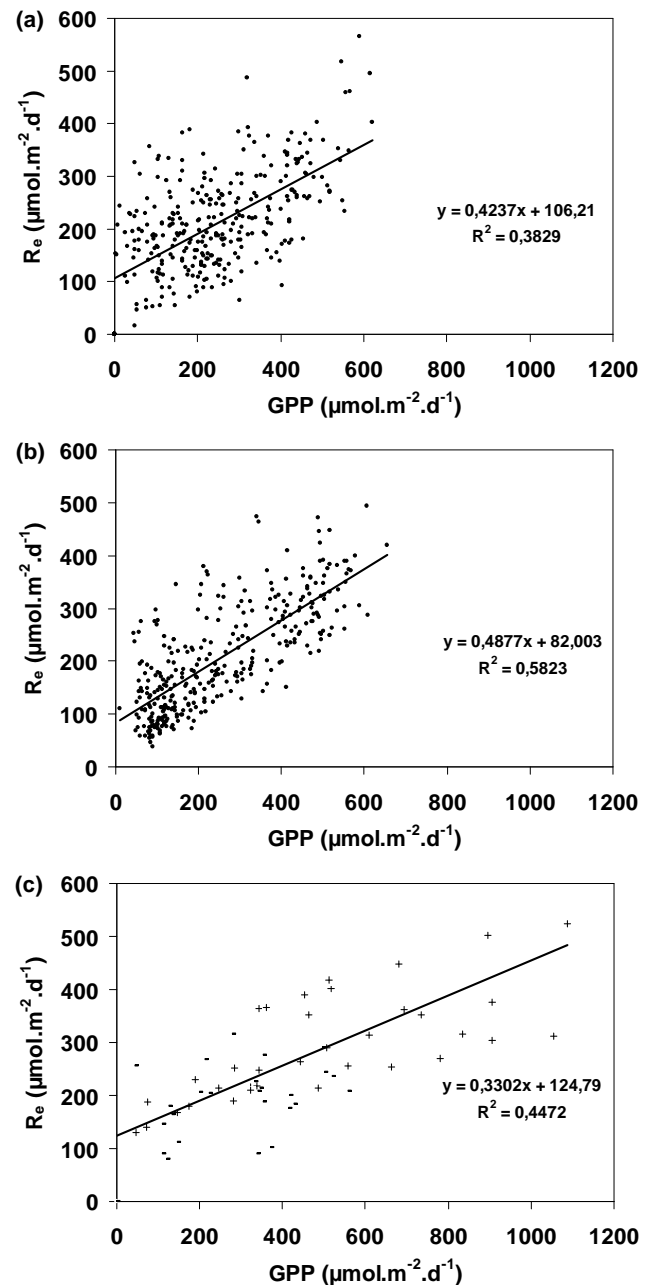
nearly linear for C<sub>4</sub> species. Thus, C<sub>4</sub> species have a higher CO<sub>2</sub> uptake than C<sub>3</sub> species in an environment with high light levels (Nippert et al., 2007). This explains the higher values of the ratio GPP/ $F_{PP}$  for the maize than for the forests (Fig. 3).

### 3.4 Dynamics and mean values of respiration

Ecosystem respiration ( $R_e$ ) results both from heterotrophic (soil micro-organisms) and autotrophic (plant) respiration (Flanagan and Johnson 2005), the latter being composed of maintenance and growth respiration. Soil temperature is the prevalent factor accountable for variations of heterotrophic respiration. Indeed, an increase of temperature favours the microbial activity responsible for soil degradation, so that heterotrophic respiration increases. This was observed at La Cape Sud during the period with bare soil, where respiration is an exponential  $Q_{10}$  function of soil temperature (Fig. 5). This tendency is commonly found for forested ecosystems (Kowalski et al., 2004; McCaughey et al., 2006), crops (Suyker et al., 2004; Moureaux et al., 2006) and grasslands (Ma et al., 2007; Kjelgaard et al., 2008).

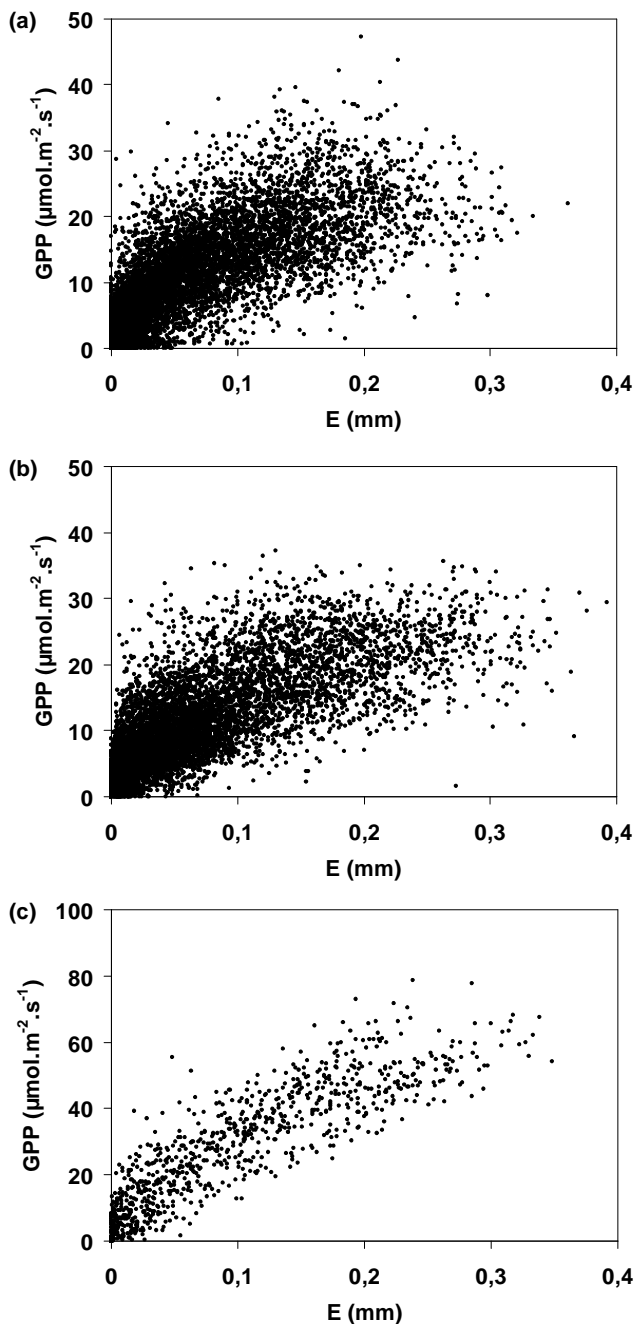
In the two forests, daily  $R_e$  is correlated to daily GPP over the whole year (Fig. 6a and 6b). This agrees with recent studies showing a close linkage between respiration and photosynthetic activity of an annual grassland (Xu and Baldocchi, 2004). However, for this ecosystem as well as for our forests, the correlation between GPP and  $R_e$  may be partially fortuitous, since factors affecting heterotrophic respiration (soil temperature) and GPP ( $F_{PP}$ ) are themselves correlated at yearly scale.

For the maize, we observe a correlation between  $R_e$  and GPP during the growth and, to a lesser extent, during the senescence (Fig. 6c), but not during the maturity phase (data not shown). During the growth, from late May to early July (Fig. 1f), soil temperature did not vary much, so that het-



**Fig. 6.** Daily ecosystem respiration ( $R_e$ ) as a linear function of daily gross primary production (GPP) for Le Bray (a), Bilos (b) and La Cape Sud (c). For the two forests (a and b), the data corresponds to the whole period of measurement. For the maize crop (c), the data is restricted to growth (crosses) and senescence (dashes).

erotrophic respiration was likely to be fairly stable. Therefore, we can conclude that the observed correlation between GPP and total ecosystem  $R_e$  during this period indeed results from a linkage between autotrophic (growth) respiration and photosynthetic activity. In this case, the latter is driven by maize physiology much more than by  $F_{PP}$ . During senescence, the correlation between GPP and total  $R_e$



**Fig. 7.** Relationship between gross primary production (GPP) and water vapour flux ( $E$ ) for Le Bray (a) and Bilos (b) during the whole period of measurement and La Cape Sud during the maturity phase of the maize (c). Note that the scale is twice as large for the maize crop.

may also be due to joint decrease in photosynthetic activity and autotrophic respiration. However, since  $F_{PP}$  and soil temperature both decrease during this period (September), the hypothesis of fortuitous correlation cannot be dismissed. During the maturity phase, the decorrelation between GPP

and total  $R_e$  results from the decrease of the former with  $F_{PP}$  while the latter remains quite stable, as soil temperature does. This suggests that  $R_e$  is dominated in this case by heterotrophic respiration, which hides a possible relationship between autotrophic (maintenance) respiration and GPP.

Mean ecosystem respiration over the whole measuring period is  $4.63 \pm 0.14$ ,  $4.52 \pm 0.13$  and  $3.40 \pm 0.14 \mu\text{mol m}^{-2} \text{s}^{-1}$  at Le Bray, Bilos and La Cape Sud, respectively (Table 2). At Le Bray, our value is close to that reported by Kowalski et al. (2004) for the same stand in 2001 ( $4.64 \pm 0.57 \mu\text{mol m}^{-2}$ ). The fact that we obtain nearly the same value for Le Bray and Bilos seems contradictory with the traditional hypothetical pattern of respiration predicting a decrease in growth respiration with tree age. This may be due to an increase of woody respiration with age, which would compensate the decrease in growth respiration. Let us note that previous studies showed an increase in  $R_e$  with stand age (Kowalski et al., 2003; Tang et al., 2008), which seems to validate our hypothesis on woody respiration.

On average over the whole measuring period,  $R_e$  of the agricultural field is slightly smaller than those of the two forests. However, it is clearly larger during the growing season of the maize, with a mean value of  $5.51 \pm 0.22 \mu\text{mol m}^{-2} \text{s}^{-1}$  and a maximum value of  $15.85 \mu\text{mol m}^{-2} \text{s}^{-1}$ . During the periods with bare soil, mean  $R_e$  is only  $1.84 \pm 0.08 \mu\text{mol m}^{-2} \text{s}^{-1}$  with maximum value of  $5.28 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Verma et al. (2005) report similar values of maximum  $R_e$  over an irrigated maize crop ( $16 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $4.5 \mu\text{mol m}^{-2} \text{s}^{-1}$  during the growing and non growing seasons, respectively). This increase in  $R_e$  during growing season may be due to an increase of autotrophic respiration or an increase of soil respiration with higher soil water content due to the irrigation. However, the second hypothesis is more coherent with the fact that total  $R_e$  is not correlated to GPP during the maturity phase of the maize. Whatever the reason, the agricultural field turns out to be a lower source of CO<sub>2</sub> during the periods with bare soil than during the vegetative season. This has an important impact on the annual carbon balance of the field (Sect. 3.6).

### 3.5 Water Use Efficiency

Water use efficiency (WUE) represents the ability of the vegetation to assimilate carbon while limiting water losses. It is defined as the ratio between GPP and  $E$ . Figure 7 shows that for a given water vapour flux, GPP is about twice as large for the maize crop at maturity as for the forests. Also, maize GPP steadily increases with  $E$  while for the two forests it tends to saturate when  $E$  exceeds 0.15 mm. These two phenomena are related to the patterns of the GPP- $g_s$  relationships (Fig. 4), since plant transpiration is directly linked with stomatal conductance  $g_s$ , although it is also a function of the water vapour density saturation deficit (see Eq. 3). The latter point is responsible for the larger scatter in the GPP- $E$  relationship than in the GPP- $g_s$  relationship.

**Table 2.** Mean and maximum daily ecosystem respiration ( $R_e$ ) expressed in  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at Le Bray, Bilos and La Cape Sud ( $\pm$  standard error estimates).

	Le Bray	Bilos	La Cape Sud (whole study period)	La Cape Sud (growing season)	La Cape Sud (non growing season)
Mean $R_e$	4.63 $\pm$ 0.14	4.52 $\pm$ 0.13	3.40 $\pm$ 0.14	5.51 $\pm$ 0.22	1.84 $\pm$ 0.08
Max $R_e$	23.16	18.44	15.85	15.85	5.28

At all sites WUE was highly variable during the measuring campaign. For the two pine forests, monthly WUE was at its minimum (approximately 3.5 and 4.5 mmol CO<sub>2</sub> mol H<sub>2</sub>O<sup>-1</sup> at Bilos and Le Bray, respectively) in June, July and August and at its maximum (around 8 and 8.5 mmol CO<sub>2</sub> mol H<sub>2</sub>O<sup>-1</sup> at Bilos and Le Bray, respectively) in November, December and January (data not shown). It is remarkable that mean WUE, over the whole year, is identical at both sites (about 5 mmol CO<sub>2</sub> mol H<sub>2</sub>O<sup>-1</sup>). Compared to other studies, this mean value of WUE is rather large. Indeed, Law et al. (2002) report annual WUE of about 3.6 mmol CO<sub>2</sub> mol H<sub>2</sub>O<sup>-1</sup> for coniferous forests and Williams et al. (2001) give 4.43 mmol CO<sub>2</sub> mol H<sub>2</sub>O<sup>-1</sup> for a ponderosa pine forest. At Le Bray, Jarosz et al. (2008) obtained 3.3 mmol CO<sub>2</sub> mol H<sub>2</sub>O<sup>-1</sup> during a dry year (2002). The difference between this value and the present one is likely to be due to the well-watered conditions which prevailed in 2007. Indeed, such conditions have a direct effect on VPD which is the main factor controlling WUE (Lamaud et al., 1996; Berbigier et al., 2001; Law et al., 2002), as can be seen in Fig. 8. As WUE increases when VPD decreases, climatic conditions explain both the difference with the results by Jarosz et al. (2008) and the seasonal evolution of WUE for our two forests, low in summer and high in winter (Fig. 8a and b). The variation of WUE with VPD observed in 2007 for Le Bray is identical to that reported by Berbigier et al. (2001) for the same stand in 1997 and 1998 (black line in Fig. 8a). This relationship was found to be also valid for the young forest (Fig. 8b). This result, together with the absence of difference for Le Bray between 1997–1998 and 2007, suggests that the WUE-VPD relationship is independent of stand age.

For the irrigated maize crop, WUE increases during growth, reaches a maximum during the maturity period (around 10 mmol CO<sub>2</sub> mol H<sub>2</sub>O<sup>-1</sup>), then decreases during senescence (data not shown). Mean WUE of the maize crop over the growing season is about 8 mmol CO<sub>2</sub> mol H<sub>2</sub>O<sup>-1</sup>. Mean WUE of the agricultural field is lower over the whole measuring period, with a value of about 4.5 mmol CO<sub>2</sub> mol H<sub>2</sub>O<sup>-1</sup>, which is very close to the WUE of the two forests at the same time scale. Of course, the lower value of WUE of the agricultural field at yearly scale is due to the long period with bare soil where there is no photosynthetic assimilation and only water losses because of soil water evaporation. When maize is at maturity, daily WUE increases when VPD

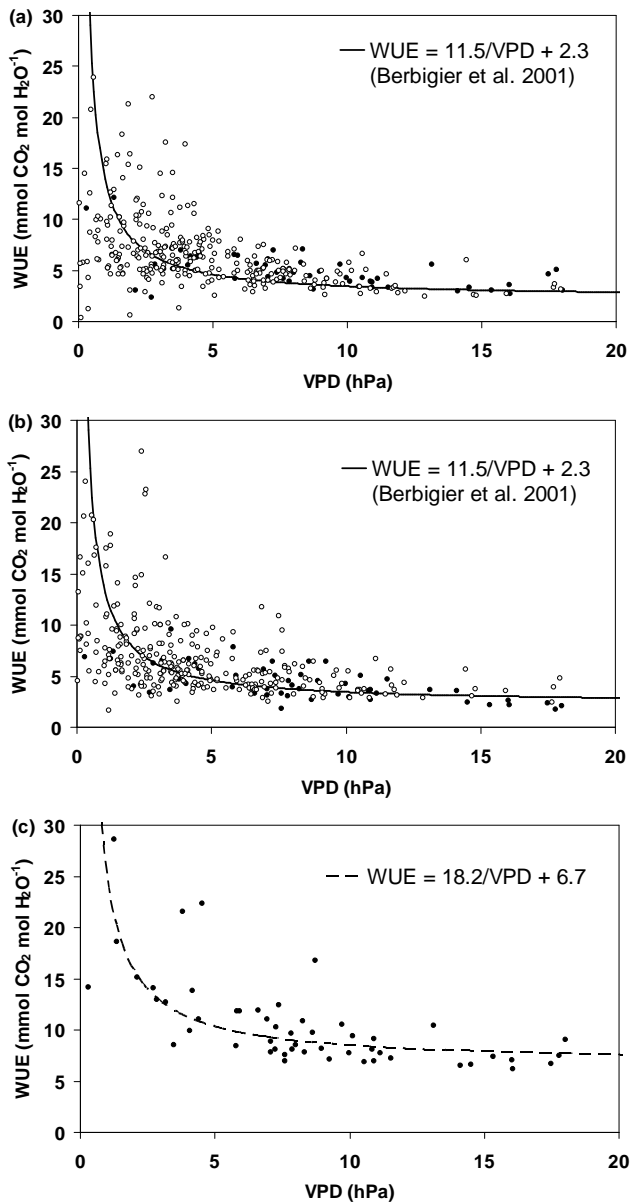
decreases, and we obtained a relationship of the same kind as for pine forests (dashed line in Fig. 8c). However, at a given value of VPD, WUE is about twice as large for maize as for pine forests, owing to the physiological advantages of C<sub>4</sub> species.

### 3.6 Carbon balance

Over the whole measurement period the three ecosystems behave as sinks of CO<sub>2</sub>, with net carbon uptake of 335, 210 and 160 g C m<sup>-2</sup> at Bilos, Le Bray and La Cape Sud, respectively (Fig. 9a).

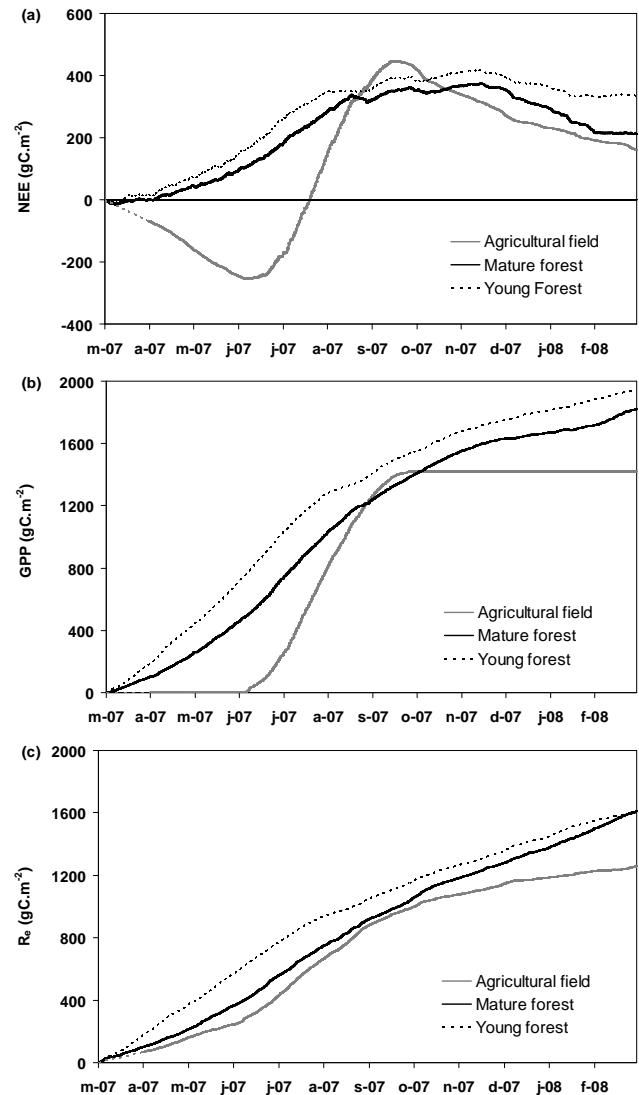
At Le Bray the value of accumulated NEE is intermediate between those reported in previous studies at this site. Indeed, NEE ranges from 57 g C m<sup>-2</sup> in 2002 (Jarosz et al., 2008) to 575 g C m<sup>-2</sup> on average in 1997 and 1998 (Berbigier et al., 2001), because of different meteorological conditions. Figure 9b and c shows that the difference between NEE of Le Bray and Bilos is due to lower GPP for the mature forest (1820 g C m<sup>-2</sup>) than for the young one (1950 g C m<sup>-2</sup>), whereas  $R_e$  is similar for the two sites (1610 g C m<sup>-2</sup> and 1615 g C m<sup>-2</sup> for Le Bray and Bilos, respectively). For both forests, our values are of the same order as those reported by Kowalski et al. (2004) for other mature maritime pine forests (GPP and  $R_e$  about 1600 and 1415 g C m<sup>-2</sup>, respectively).

Figure 9b also shows that the annual dynamics of accumulated GPP are different for the two forests, probably owing to differences in the relative contribution of understoreys to total ecosystem CO<sub>2</sub> fluxes. In a study over eleven forests at different latitudes and longitudes, Misson et al. (2007) showed that the contribution of understoreys varied between 0% and 39% of total ecosystem GPP. In the present case the observed differences between the two forests seem to be related to the understorey phenology. For the mature forest, the slope of accumulated GPP increases during summer, which is the only period when the understorey, composed of grasses, is physiologically active. For the young forest, accumulated GPP is larger from the very beginning of the measurement period (early March), which is coherent with the fact that its understorey, composed of heathers and gorses, is perennial. All along the year the occasional decreases in GPP accumulation rate are due, for the young forest, to the period of water stress in early August (Sect. 3.2), and for both forests,



**Fig. 8.** Daily water use efficiency (WUE) as a function of daily vapour pressure deficit (VPD) for Le Bray (a), Bilos (b) and La Cape Sud during the maturity phase of the maize (c). For all sites, filled symbols correspond to data from 11 July to 1 September (period of maturity of the maize during summer); for the two forests, open symbols represent data from the rest of the year. The solid lines in (a) and (b) correspond to the function obtained by Berbigier et al. (2001) at Le Bray ( $WUE=11.5/VPD+2.3$ ) and the dashed line in (c) corresponds to the function obtained here for maize at maturity ( $WUE=18.2/VPD+6.7$ ).

to the decrease of global radiation in winter, that affects the whole ecosystem (i.e. understorey and overstorey). It has to be pointed out that the dynamics of ecosystem respiration is similar (Fig. 9c), which supports the hypothesis of a relationship between autotrophic respiration and GPP (Sect. 3.4).



**Fig. 9.** (a) Accumulated net ecosystem exchange (NEE), (b) accumulated gross primary production (GPP) and (c) accumulated ecosystem respiration ( $R_e$ ) for Le Bray (black line), Bilos (dotted line) and La Cape Sud (grey line). For La Cape Sud, where measurements only began at the end of March 2007 (Fig. 1e), GPP of this month was assumed to be zero, as in April and May, and accumulated NEE and  $R_e$  (with  $NEE=R_e$ ) were estimated by extrapolating the slope of values from the first week of April (dashed lines in panels a and c).

Over the whole measuring period, accumulated GPP of the agricultural field is  $1420 \text{ g C m}^{-2}$  (Fig. 9b), which is only 22% lower than for the mature forest and 27% lower than for the young one. The high value of the accumulated GPP of the agricultural field at yearly scale results from the strong carbon uptake of the maize crop from late June to early September. This is in agreement with previous studies reporting accumulated GPP between  $1100$  and  $1750 \text{ g C m}^{-2}$  for other agricultural fields occupied by maize only during spring and

summer (Suyker et al., 2004, 2005). Owing to the high GPP of the maize crop, the accumulated NEE of the agricultural field in September is slightly higher than those of the two forests (Fig. 9a). Since the field becomes a CO<sub>2</sub> source after the maize harvest, the accumulated NEE progressively decreases from October to February. However, it is still high at the end of the measuring period, only 24% lower than for the mature forest. In addition to the high GPP of the maize crop during summer, the fact that the agricultural field is nearly as important a sink as the mature forest at yearly scale is due to its lower accumulated  $R_e$  (1260 g C m<sup>-2</sup>, Fig. 9c), resulting from low respiration rates during the long period with bare soil (Sect. 3.4).

Comparison of the annual carbon balance of different ecosystems is generally performed on the basis on their Net Biome Production, including the carbon export resulting from harvest. However, comparison of NBP of our agricultural field and our two pine stands is not feasible at yearly scale. Indeed, pine forests of the Les Landes region, dedicated to biomass production for heating, woodwork or paper manufacturing, are of course not harvested as the same time scale as crops. They generally sustain several clearings during the first twenty years and a complete harvest after about 40 years. Therefore, comparisons of carbon balance of agricultural fields and pine stands, based on NBP, can only be performed at the scale of the life cycle of the trees. However, to allow the reader to get a true sense of the annual carbon balance of our agricultural field (i.e the NBP of the field at yearly scale), we have determined (following Hollinger et al., 2005) the amount of carbon removed from grain harvest. Based on a production of 140 q ha<sup>-1</sup>, the carbon export of the field is -530 g C m<sup>-2</sup>, so that its NBP is -370 g C m<sup>-2</sup> (with NEE=+160 g C m<sup>-2</sup>). This means that the field lost carbon during this year when it was sown with maize. Of course, it may also gain carbon during other years when sown with other species, which strengthens the fact that comparisons with forests can only be performed at larger time scales.

#### 4 Summary and conclusions

The study presented in this paper aimed to characterize the respective contribution of various ecosystems, in similar climatic and weather conditions, to global carbon dioxide and water vapour exchanges. With this end in view, we analysed flux measurements performed simultaneously during one year above three ecosystems of the Les Landes region, in South-West France: an agricultural field with maize from 29 May to 18 October, a 5 year-old maritime pine forest and a 37 year-old maritime pine forest.

We observed how gross primary production (GPP) of the two forests during the whole period, and of the maize crop during summer, were related to climatic conditions, with a predominant role of vapour pressure deficit (VPD) for forests and of photosynthetic photon flux density ( $F_{PP}$ ) for maize.

Large differences in GPP between the two forests were observed during the first three weeks of August, a quite long period without rainfall, when the soil water content of the young stand dropped below a critical level (12% at 0.8 m depth) inducing stomatal closure of the trees.

It was also found that the annual variation of GPP was more marked for the mature forest than for the young one. This is likely to be due to differences in the understorey vegetation, which is perennial in the young forest and seasonal in the mature one. However, GPP was of the same order for the two forests and about twice as low as for the maize at maturity. This mainly arises from physiological differences between C<sub>3</sub> and C<sub>4</sub> species, resulting in photosynthetic limitations of the former under high light intensity.

Although the maize crop at maturity is a more important sink for CO<sub>2</sub>, the perennial physiological activity of the forests results in larger accumulated GPP and NEE at yearly scale. Nevertheless, annual accumulated GPP and NEE of the agricultural field are only 22% and 24% lower, respectively than those of the mature forest. Annual accumulated NEE of the mature forest is 37% lower than the one of the young forest, merely because of an accumulated GPP lower by 7%, whereas their accumulated  $R_e$  are similar.

The analysis of water losses in relation to photosynthetic assimilation, through the Water Use Efficiency, showed that WUE increases with VPD for the three ecosystems, but is about twice as large for the maize at maturity as for the two forests. No difference was observed in the WUE-VPD relationship between the young and the mature forests, which suggests that this relationship is independent of stand age.

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#### References

- Aubinet, M., Grelle, A., Ibrom, A., Rannik, U., Moncrieff, J., Foken, T., Kowalski, A. S., Martin, P. H., Berbigier, P., Bernhofer, C., Clement, R., Elbers, J., Granier, A., Grünwald, T., Morgenstern, K., Pilegaard, K., Rebmann, C., Snijders, W., Valentini, R., and Vesala, T.: Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology, *Adv. Ecol. Res.*, 30, 113–175, 2000.
- Baldocchi, D. D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., Anthoni, P., Berhofer, C., Davis, K., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X., Malhi, Y., Meyers, T., Munger, J. W., Oechel, W., Pilegaard, K., Schmid, H. P., Valentini, R., Verma, S., Vesala, T., Wilson, K., and Wofsy, S.: FLUXNET: a new tool to study the temporal and spatial variability

- ity of ecosystem-scale carbon dioxide, water vapor and energy flux densities, *B. Am. Meteorol. Soc.*, 82, 2415–2434, 2001.
- Berbigier, P., Bonnefond, J. M., and Mellmann, P.: CO<sub>2</sub> and water vapour fluxes for 2 years above Euroflux forest site, *Agr. Forest. Meteorol.*, 108, 183–197, 2001.
- Burba, G. G., McDermitt, D. K., Grelle, A., Anderson, D. J., and Xu, L.: Addressing the influence of instrument surface heat exchange on the measurements of CO<sub>2</sub> flux from open-path gas analyzers, *Global Change. Biol.*, 14, 1854–1876, 2008.
- Dolman, A. J., Noilhan, J., Durand, P., Sarrat, C., Brut, A., Butet, A., Jarosz, N., Brunet, Y., Loustau, D., Lamaud, E., Tolk, L., Ronda, R., Miglietta, F., Gioli, B., Enzo, M., Esposito, M., Gerbig, C., Körner, S., Galdemard, P., Ramonet, M., Ciais, P., Neininger, B., Hutjes, R. W. A., Elbers, J. A., Warnecke, T., Landa, G. P., Sanz, M., Scholz, Y., and Facon, G.: CERES, the CarboEurope Regional Experiment Strategy in les Landes, South West France, May–June 2005, *B. Am. Meteorol. Soc.*, 87, 1367–1379, 2006.
- Falge, E., Tenhunen, J., Baldocchi, D., Aubinet, M., Bakwin, P., Berbigier, P., Bernhofer, C., Bonnefond, J. M., Burba, G., Clement, R., Davis, K. J., Elbers, J. A., Falk, M., Goldstein, A. H., Grelle, A., Granier, A., Grünwald, T., Gudmundsson, J., Hollinger, D., Janssens, I. A., Keronen, P., Kowalski, A. S., Katul, G., Law, B. E., Malhi, Y., Meyers, T., Monson, R. K., Moors, E., Munger, J. W., Oechel, W., Paw, U. K. T., Pilegaard, K., Rannik, U., Rebmann, C., Suyker, A., Thorgeirsson, H., Tirone, G., Turnipseed, A., Wilson, S., and Wofsy, S.: Phase and amplitude of ecosystem carbon release and uptake potentials as derived from FLUXNET measurements, *Agr. Forest. Meteorol.*, 113, 75–95, 2002.
- Farquhar, G. D., Von Caemmerer, S., and Berry, J. A.: A Biochemical Model of Photosynthetic CO<sub>2</sub> Assimilation in Leaves of C<sub>3</sub> Species, *Planta.*, 149, 78–90, 1980.
- Flanagan, L. B. and Johnson, B. G.: Interacting effects of temperature, soil moisture and plant biomass production on ecosystem respiration in a northern temperate grassland, *Agr. Forest. Meteorol.*, 130, 237–253, 2005.
- Foken, T. and Wichura, B.: Tools for quality assessment of surface-based flux measurements, *Agr. Forest. Meteorol.*, 78, 83–105, 1996.
- Hollinger, S. E., Bernacchi, C. J., and Meyers, T. P.: Carbon budget of mature no-till ecosystem in North Central Region of the United States, *Agr. Forest. Meteorol.*, 130, 59–69, 2005.
- IPCC: Climate Change 2001: The scientific Basis. Contribution of Working Group I to the third assessment report of the Intergovernmental Panel on Climate Change, Cambridge University Press, USA, 2001.
- IPCC: Climate Change 2007: The physical science Basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change, Cambridge University Press, USA, 2007.
- Jarosz, N., Brunet, Y., Lamaud, E., Irvine, M., Bonnefond, J. M., and Loustau, D.: Carbon dioxide and energy flux partitioning between the understorey and the overstorey of a maritime pine forest during a year with reduced soil water availability, *Agr. Forest. Meteorol.*, 148, 1508–1523, 2008.
- Kaimal, J. C. and Finnigan, J. J.: Atmospheric Boundary Layer Flows, their Structure and Measurements, Oxford University Press, UK, 1994.
- Kjelgaard, J. F., Heilman, J. L., McInnes, K. J., Owens, M. K., and Kamps, R. H.: Carbon dioxide exchange in a subtropical, mixed C<sub>3</sub>/C<sub>4</sub> grassland on the Edwards Plateau, Texas, *Agr. Forest. Meteorol.*, 148, 953–963, 2008.
- Kowalski, A. S., Loustau, D., Berbigier, P., Manca, G., Tedeschi, V., Borghetti, M., Valentini, R., Kolari, P., Berniger, F., Rannik, U., Hari, P., Rayment, M., Mencuccini, M., Moncrieff, J., and Grace, J.: Paired comparison of carbon exchange between undisturbed and regenerating stands in four managed forests in Europe, *Global. Change. Biol.*, 10, 1707–1723, 2004.
- Kowalski, S., Sartore, M., Burrett, R., Berbigier, P., and Loustau, D.: The annual carbon budget of a French pine forest (*Pinus pinaster*) following harvest, *Global. Change. Biol.*, 9, 1051–1065, 2003.
- Lamaud, E., Brunet, Y., and Berbigier, P.: Radiation and water use efficiencies of two coniferous forest canopies, *Phys. Chem. Earth*, 21, 361–365, 1996.
- Law, B. E., Falge, E., Gu, L., Baldocchi, D. D., Bakwin, P., Berbigier, P., Davis, K., Dolman, A. J., Falk, M., Fuentes, J. D., Goldstein, A., Granier, A., Grelle, A., Hollinger, D., Janssens, I. A., Jarvis, P., Jensen, N. O., Katul, G., Mahli, Y., Matteucci, G., Meyers, T., Monson, R., Munger, W., Oechel, W., Olson, R., Pilegaard, K., Paw, K. T., Thorgeirsson, H., Valentini, R., Verma, S., Vesala, T., Wilson, K., and Wofsy, S.: Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation, *Agr. Forest. Meteorol.*, 113, 97–120, 2002.
- Ma, S., Baldocchi, D. D., Xu, L., and Hehn, T.: Inter-annual variability in carbon dioxide exchange of an oak/grass savanna and open grassland in California, *Agr. Forest. Meteorol.*, 147, 157–171, 2007.
- Massman, W. J.: A simple method for estimating frequency response corrections for eddy covariance systems, *Agr. Forest. Meteorol.*, 104, 185–198, 2000.
- McCaughy, J. M., Pejam, M. R., Arain, M. A., and Cameron, D. A.: Carbon dioxide and energy fluxes from a boreal mixedwood forest ecosystem in Ontario, Canada, *Agr. Forest. Meteorol.*, 140, 79–96, 2006.
- Misson, L., Baldocchi, D. D., Black, T. A., Blanken, P. D., Brunet, Y., Curiel Yuste, J., Dorsey, J. R., Falk, M., Granier, A., Irvine, M. R., Jarosz, N., Lamaud, E., Launiainen, S., Law, B. E., Longdoz, B., Loustau, D., McKay, M., Paw U, K. T., Vesala, T., Vickers, D., Wilson, K. B., and Goldstein, A. H.: Partitioning forest carbon fluxes with overstorey and understorey eddy-covariance measurements: A synthesis based on FLUXNET data, *Agr. Forest. Meteorol.*, 144, 14–31, 2007.
- Moncrieff, J. B., Massheder, J. M., de Bruin, H., Elbers, J., Friborg, T., Heusinkveld, B., Kabat, P., Scott, S., Soegaard, H., and Verhoef, A.: A system to measure surface flux momentum, sensible heat, water vapor and carbon dioxide, *J. Hydrol.*, 188–189, 589–611, 1997.
- Monteith, J. L.: Evaporation and surface temperature, *Q. J. Roy. Meteorol. Soc.*, 107, 1–27, 1981.
- Moore, C. J.: Frequency Response Corrections for Eddy Correlation Systems, *Bound.-Lay. Meteorol.*, 37, 17–35, 1986.
- Moureaux, C., Debacq, A., Bodson, B., Heinesch, B., and Aubinet, M.: Annual net ecosystem carbon exchange by a sugar beet crop, *Agr. Forest. Meteorol.*, 139, 25–39, 2006.
- Nippert, J. B., Fay, P. A., and Knapp, A. K.: Photosynthetic traits in C<sub>3</sub> and C<sub>4</sub> grassland species in mesocosm and field environ-

- ments, *Environ. Exp. Bot.*, 60, 412–420, 2007.
- Ogée, J., Lamaud, E., Brunet, Y., Berbigier, P., and Bonnefond, J. M.: A long-term study of soil heat flux under a forest canopy, *Agr. Forest. Meteorol.*, 106, 173–186, 2001.
- Romberger, J. A., Hejnowicz, Z., and Hill, J. F.: *Plant structure: function and development. A treatise on anatomy and vegetative development, with special reference to woody plants*, The Blackburn press, Caldwell, USA, 1993.
- Steduto, P. and Hsiao, T. C.: Maize canopies under two soil water regimes. I. Diurnal patterns of energy balance, carbon dioxide flux, and canopy conductance, *Agr. Forest. Meteorol.*, 89, 169–184, 1998a.
- Steduto, P. and Hsiao, T. C.: Maize canopies under two soil water regimes. III. Variation in coupling with the atmosphere and the role of leaf area index, *Agr. Forest. Meteorol.*, 89, 201–213, 1998b.
- Suyker, A. E., Verma, S. B., Burba, G. G., and Arkebauer, T. J.: Gross primary production and ecosystem respiration of irrigated maize and irrigated soybean during a growing season, *Agr. Forest. Meteorol.*, 131, 180–190, 2005.
- Suyker, A. E., Verma, S. B., Burba, G. G., Arkebauer, T. J., Walters, D. T., and Hubbard, K. G.: Growing season carbon dioxide exchange in irrigated and rainfed maize, *Agr. Forest. Meteorol.*, 124, 1–13, 2004.
- Tang, J., Bolstad, P. V., Desai, A. R., Martin, J. G., Cook, B. D., Davis, K. J., and Carey, E. V.: Ecosystem respiration and its components in an old-growth forest in the Great Lakes region of the United States, *Agr. Forest. Meteorol.*, 148, 171–185, 2008.
- Verma, S. B., Dobermann, A., Cassman, K. G., Walters, D. T., Knops, J. M., Arkebauer, T. J., Suyker, A. E., Burba, G. G., Amos, B., Yank, H., Ginting, D., Hubblard, K. G., Gitelson, A. A., and Walter-Shea, E. A.: Annual carbon dioxide exchange in irrigated and rainfed maize-based agroecosystems, *Agr. Forest. Meteorol.*, 131, 77–96, 2005.
- Vickers, D. and Mahrt, L.: Quality Control and Flux Sampling Problems for Tower and Aircraft Data, *J. Atmos. Ocean. Tech.*, 14, 512–526, 1997.
- Webb, E. H., Pearman, G. I., and Leuning, R.: Correction of flux measurements for density effects due to heat and water transfer, *Q. J. Roy. Meteorol. Soc.*, 106, 85–100, 1980.
- Williams, M., Law, B. E., Anthoni, P. M., and Unsworth, M. H.: Use of a simulation model and ecosystem data to examine carbon-water interactions in ponderosa pine, *Tree. Physiol.*, 21, 287–298, 2001.
- Xu, L. and Baldocchi, D. D.: Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California, *Agr. Forest. Meteorol.*, 123, 79–96, 2004.