**Biogeosciences
Discussions**

**CO$_2$ and water
exchanges over three
agroecosystems**

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Simultaneous measurements of CO$_2$ and water exchanges over three agroecosystems in South-West France

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CO$_2$ and water exchanges over three agroecosystems

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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 from 31 March 2007 to 3 March 2008 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$_2$, 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$_2$ sinks with carbon storage of about 500, 330 and 230 gC m^{-2} for the young forest, the mature forest and the agricultural field, respectively. 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$_4$ 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_2 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.

In the present study, we report simultaneous measurements of water vapour (H_2O) and carbon dioxide (CO_2) fluxes performed with the eddy-covariance method during nearly one year 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 (Re), (ii) to character-

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ize 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^{-1}. The understorey vegetation consists essentially of grasses (*Molinia coerula* 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*

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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 ta-
5 ble 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
10 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 and 18 October 2007. The plot was irrigated from June to August by two ramps, with a 400 m radius in the west direction and a 350 m radius in
15 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
20 Bray and a Young 81000V – R. M. Young Company, Traverse City, Michigan, USA – at Bilos and La Cape Sud) coupled with CO_2/H_2O 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_2O and CO_2 are collected
25 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_2, H_2O, T).

At each site net radiation (R_n) is measured with a NrLite Pyrradiometer (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 (PPFD) 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 1, 2, 4, 8, 16, 32, 64 and 100 cm 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 5 and 10 cm and four temperature profiles were set up at 1, 2, 4, 8, 16, 32, 64 and 100 cm 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 1, 5, 10, 20, 30, 40 and 100 cm using 7 homemade thermocouples. SWC was measured at 0.10, 0.20, 0.30 and 0.40 m using 4 CS616 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" (Corvallis, 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 effect of density fluctuations (Webb et al., 1980).

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$_2$ flux

Net Ecosystem Exchange (NEE) was partitioned between Gross Primary Production (GPP) and Ecosystem Respiration (Re). Following Kowalski et al. (2003, 2004), daytime NEE (NEE$_d$) was expressed as a curvilinear function of the photosynthetic photon flux density (PPFD):

$$\text{NEE}_d = \frac{a_1 \text{PPFD}}{a_2 + \text{PPFD}} + \text{Re}_d \tag{1}$$

where Re$_d$ 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. Re$_d$, a_1 and a_2 were determined daily by non-linear regression. GPP was thus calculated half hourly using a_1, a_2 and PPFD. Half hourly values of Re$_d$ were obtained by difference between NEE and GPP.

Provided that turbulent mixing is sufficient ($u_* > 0.2\,\mathrm{m\,s^{-1}}$), measurements of night-time NEE (NEE_n) directly give nighttime respiration (Re_n). In order to estimate Re_n in low turbulence conditions, data for $u_* > 0.2\,\mathrm{m\,s^{-1}}$ were fitted to an exponential Q_{10} function of soil temperature as:

$$\mathrm{Re}_n = \mathrm{Re}_{n,15} Q_{10}^{(Ts-15)/10} \tag{2}$$

where $\mathrm{Re}_{n,15}$ is the nighttime respiration flux at a reference temperature ($T_s = 15\,°\mathrm{C}$) and Q_{10} is the sensitivity to temperature.

2.3.3 Estimating stomatal conductance

The stomatal conductance (g_s) can be determined from the water vapour flux by inverting the Penman-Monteith equation (Monteith and Unsworth, 1990):

$$g_s = \frac{D_{CO_2}}{D_{H_2O}} \frac{\frac{E}{\mathrm{VPD}}}{1 + \frac{E}{\mathrm{VPD}}(R_a + R_b)\left(\frac{\beta s}{\gamma} - 1\right)} \tag{3}$$

where D_{CO_2} and D_{H_2O} ($\mathrm{m^2\,s^{-1}}$) are the molecular diffusivity for CO_2 and water vapour, respectively ($D_{CO_2}/D_{H_2O} \approx 0{,}62$), E is the water vapour flux ($\mathrm{kg\,m^{-2}\,s^{-1}}$), VPD the water vapour density saturation deficit ($\mathrm{kg\,m^{-3}}$), β the Bowen ratio, s the slope of the saturation curve ($\mathrm{Pa\,K^{-1}}$), γ the psychrometric constant ($\mathrm{Pa\,K^{-1}}$) and R_a and R_b the aerodynamic and boundary layer resistances ($\mathrm{s\,m^{-1}}$), 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 PPFD 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 $30\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$) and a minimum in December. These annual
variations are related to those of PPFD (Fig. 1a), since solar radiation is the dominant environmental factor controlling CO_2 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) in early April 2007, which may be due to the difference between the understoreys of the two stands (Sect. 2.1.1 and 2.1.2). Secondly, a large difference appears during the first two weeks of August, when the NEE of Bilos suddenly decreases to $10\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ (Fig. 1d) whereas the NEE of Le Bray remains stable
(Fig. 1c). This feature is probably due to the absence of rainfall during this period (Fig. 1b), which would induce a high water stress for the young forest, but not for the mature one. This point is detailed in the next section.

Regarding the agricultural field, the dynamics of NEE (Fig. 1e) is essentially controlled by the phenology of the maize (Fig. 1f). The site is a source of CO_2 during the
period with bare soil (from 31 March to 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 $60\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ 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, that starts around the 1st September, accelerates the decrease of NEE. The field becomes again a source of CO_2 from late September, although maize is harvested only after
5 mid-October.

3.2 Factors affecting GPP

This section focusses on the period from 28 July 2007 (DOY 209) to 18 August 2007 (DOY 230), marked by the absence of rainfall (in fact since DOY 205), but during which the maize crop was irrigated. Figure 2 presents time series of PPFD, VPD and GPP
10 recorded at each site.
At the beginning of the period, GPP is of the same order for the two forests and appears stable from DOY 209 to 211 (Fig. 2c and d). On DOY 212 GPP decreases at both sites, but more strongly for the young forest of Bilos. As the decrease is induced by stomatal closure, following the increase in VPD (Fig. 2b), this difference suggests
15 that the young stand is more sensitive to water deficit, due to the absence of rainfall, than the mature forest. Also, GPP at Bilos does not increase as strongly as at Le Bray with the decrease in VPD on DOY 213, and it remains low until the end of this dry period. From DOY 214 to 217, we observe at both sites a decrease in GPP related to a progressive increase in VPD, PPFD remaining approximately at the same level.
20 Then, with the sharp fall of VPD on DOY 218, GPP of both forests slightly increases again, despite very low PPFD. During the rest of the dry period, the dynamics of GPP at both sites is less marked because of the relative stability of both VPD and PPFD. 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
25 for water exceeding soil-plant hydraulic system provokes stomatal closure, inducing a decrease in GPP.
For the young forest, this phenomenon is amplified by water stress effects. As indicated in Table 1, accumulated GPP at Bilos is 58% lower over the period from DOY

205 to 230 than over the previous well-watered period of 26 days, while at Le Bray it is only 12% lower. This strong decrease in GPP of the young forest is due to the decrease in SWC with the absence of rainfall. Indeed, a decrease in SWC, inducing a lower maximum sustainable water flux, provokes stomatal closure in order to limit water losses (Williams et al., 2001). However, water stress effects are not visible for the mature forest of Le Bray, where SWC still decreases as for Bilos with the absence of rainfall. This is probably due to better root prospection in the mature forest, which allows the trees to extract water from deeper layers.

Contrary to the two forests, the maize crop (Fig. 2e) is not sensitive to the variations in VPD. Indeed, from DOY 209 to 217, the variations in GPP are not correlated with those of VPD. Owing to irrigation, the maize is able to ensure a continuous supply of water in response to the high air evaporative demand. On the other hand, GPP of the maize crop strongly varies with PPFD, as can be clearly seen in the period from DOY 217 to 222. No such correlation between GPP and PPFD is visible for the two forests (GPP even slightly increases on DOY 218). This point is discussed in the next section.

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 agreement with those from Verma et al. (2005) who observed that peak CO_2 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_2 uptake is achieved by crops (especially C_4 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 a short time 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 $1.9\,m^2\,m^{-2}$, for maize, mature and young forests, respectively), and recent studies have shown a high positive correlation between GPP and LAI (Steduto and Hsiao, 1998a, 1998b; 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. 3 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. 3a and b) than for the maize (Fig. 3c). This is due to physiological differences between C_3 (pines) and C_4 (maize) species. CO_2 fixation for C_3 species is catalysed by ribulase biphosphate carboxylase (RuBPCase). However, this enzyme is equally able to fix O_2, so that CO_2 and O_2 are in competition. For C_4 species, CO_2 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_2 and O_2. Furthermore, PEPCase have a better affinity to CO_2 than RuBPCase. Moreover, C_3 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_3 species is a curvilinear function of stomatal conductance (g_s), while it is nearly linear for C_4 species. Thus, C_4 species have a higher CO_2 uptake than C_3 species in an environment with high light levels (Nippert et al., 2007). This explains why we observed a
5 strong response of GPP to PPFD for the maize (Fig. 2e) but not for the forests (Fig. 2c and d).

3.4 Dynamics and mean values of respiration

Ecosystem respiration (Re) results both from heterotrophic (soil micro-organisms) and autotrophic (plant) respiration (Flanagan and Johnson, 2005), the latter being com-
10 posed 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
15 (Fig. 4). 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 Re is correlated to daily GPP over the whole year (Fig. 5a and b). This agrees with recent studies showing a close linkage between respiration
20 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 Re may be partially fortuitous, since factors affecting heterotrophic respiration (soil temperature) and GPP (PPFD) are themselves correlated at yearly scale.

For the maize, we observe a correlation between Re and GPP during the growth
25 and, to a lesser extent, during the senescence (Fig. 5c), 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 heterotrophic respiration was likely to be fairly stable. Therefore, we can conclude that the observed correlation between GPP and to-

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tal ecosystem Re 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 PPFD. During senescence, the correlation between GPP and total Re may also be due to joint decrease in photosynthetic activity and autotrophic respiration. However, since PPFD 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 Re results from the decrease of the former with PPFD while the latter remains quite stable, as soil temperature does. This suggests that Re 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 -4.20 ± 0.12, -3.84 ± 0.11 and $-3.40\pm0.14\,\mu mol\,m^{-2}\,s^{-1}$ 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 ($-4.64\pm0.57\,\mu mol\,m^{-2}$). The fact that we obtain a higher value for Le Bray than for Bilos is coherent with previous studies which showed an increase in Re with stand age (Kowalski et al., 2003; Tang et al., 2008). This seems contradictory with the traditional hypothetical pattern of respiration predicting a decrease in growth respiration with tree age, but may be due to an increase of woody respiration with age.

On average over the whole measuring period, Re 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 $-5.51\pm0.22\,\mu mol\,m^{-2}\,s^{-1}$ and a maximum value of $-15.85\,\mu mol\,m^{-2}\,s^{-1}$. During the periods with bare soil, mean Re is only $-1.84\pm0.08\,\mu mol\,m^{-2}\,s^{-1}$ with maximum value of $-5.28\,\mu mol\,m^{-2}\,s^{-1}$. Verma et al. (2005) report similar values of maximum Re over an irrigated maize crop ($-16\,\mu mol\,m^{-2}\,s^{-1}$ and $-4.5\,\mu mol\,m^{-2}\,s^{-1}$ during the growing and non growing seasons, respectively). This increase in Re during growing season may be due to an increase of autotrophic respiration or an increase of soil respiration with higher soil wa-

ter content due to the irrigation. However, the second hypothesis is more coherent with the fact that total Re 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_2 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 6 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. 3), since plant transpiration is directly linked with stomatal conductance g_s, although it is also a function of VPD (see Eq. 3). The latter point is responsible for the larger scatter in the GPP-E relationship than in the GPP-g_s relationship.

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_2 mol H_2O^{-1} at Bilos and Le Bray, respectively) in June, July and August and at its maximum (around 8 and 8.5 mmol CO_2 mol H_2O^{-1} 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_2 mol H_2O^{-1}). 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_2 mol H_2O^{-1} for coniferous forests and Williams et al. (2001) give 4.43 mmol CO_2 mol H_2O^{-1} for a ponderosa pine forest. At Le Bray, Jarosz et al. (2008) obtained 3.3 mmol CO_2 mol H_2O^{-1} 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. 7. 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. 7a 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 (solid line in Fig. 7a). This relationship was found to be also valid for the young forest (Fig. 7b). 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 $10\,\mathrm{mmol\,CO_2\,mol\,H_2O^{-1}}$), then decreases during senescence (data not shown). Over the whole growing season, WUE of the agricultural field is about $8\,\mathrm{mmol\,CO_2\,mol\,H_2O^{-1}}$. 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. 7c), 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$_4$ species.

3.6 Carbon balance

Over the whole measurement period the three ecosystems behave as sinks of CO$_2$, with net carbon uptake of 500, 330 and $230\,\mathrm{gC\,m^{-2}}$ at Bilos, Le Bray and La Cape Sud, respectively (Fig. 8a).

At Le Bray the value of accumulated NEE is intermediate between those reported in previous studies at this site. Indeed, NEE ranges from $57\,\mathrm{gC\,m^{-2}}$ in 2002 (Jarosz et al., 2008) to $575\,\mathrm{gC\,m^{-2}}$ on average in 1997 and 1998 (Berbigier et al., 2001), because of different meteorological conditions. Figure 8b and c shows that the difference between NEE of Le Bray and Bilos is due both to higher Re and lower GPP for the mature forest (Re=$-1445\,\mathrm{gC\,m^{-2}}$ and GPP=$1775\,\mathrm{gC\,m^{-2}}$) than for the young one

(Re=-1315 gC m^{-2} and GPP=1815 gC m^{-2}). 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 Re about 1600 and -1415 gC m^{-2}, respectively).

Although the values of accumulated GPP are very close for the two forests, their annual dynamics are different (Fig. 8b), probably owing to differences in the relative contribution of understoreys to total ecosystem CO_2 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 April), 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, 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. 8c), which supports the hypothesis of a relationship between autotrophic respiration and GPP (Sect. 3.4).

Over the whole measuring period, accumulated GPP of the agricultural field is 1420 gC m^{-2} (Fig. 8b), which is only about 20% lower than for the two forests. 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 gC 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. 8a). Since the field becomes a CO_2 source after the maize harvest, the

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accumulated NEE progressively decreases from October to February. However, it is still high at the end of the measuring period, only 30% 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 Re ($-1190\,\mathrm{gC\,m^{-2}}$, Fig. 8c), resulting from low respiration rates during the long period with bare soil (Sect. 3.4).

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 from 31 March 2007 to 3 March 2008 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 global radiation (R_g) for maize. Large differences in GPP between the two forests were observed during three weeks from late July to mid-August. This period was marked by the absence of rainfall, which induced a high water stress for the young stand but not for the mature one where, owing to better root prospection, trees are able to extract water from deeper layers.

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_3 and C_4 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_2, the perennial physiological activity of the forests results in larger accumulated GPP and NEE at yearly scale. Nevertheless, annual accumulated GPP is only 20% lower for the agricultural field than for the two forests. Though annual accumulated GPP of the two forests were found to be similar, annual accumulated NEE of the mature one was lower because of a higher respiration rate, which may be due to an increase in woody respiration with tree age. Because of the high respiration rate of the mature forest, its annual cumulated NEE is only 30% higher than the one of the agricultural field.

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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Table 1. Total rainfall (mm) and accumulated gross primary production (gC m^{-2}) at Le Bray, Bilos and La Cape Sud during well-watered (from DOY 179 to DOY 204) and no rainfall (from DOY 205 to DOY 230) 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 179 to 204	31.0	29.6	163.6	174.1	148.4	332.1
DOY 205 to 230	0	0	122.4	153.6	62.3	296.9

Table 2. Mean and maximum daily ecosystem respiration (Re) expressed in μmol m^{-2} s^{-1} at Le Bray, Bilos and La Cape Sud (±standard error estimates).

	Le Bray	Bilos	La Cape Sud (whole study period)	La Cape Sud (growing season)	La Cape Sud (non growing season)
Mean Re	−4.20±0.12	−3.84±0.11	−3.40±0.14	−5.51±0.22	−1.84±0.08
Max Re	−14.45	−9.67	−15.85	−15.85	−5.28
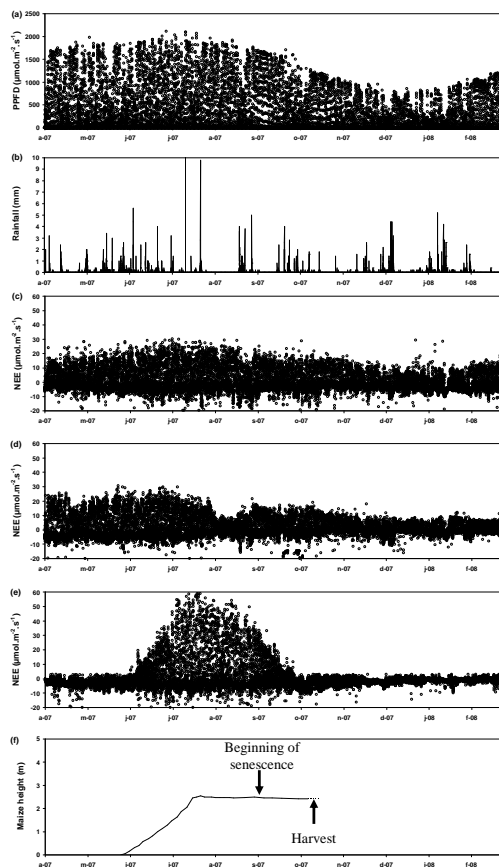
Fig. 1. Half-hourly values of photosynthetic photon flux density (PPFD) **(a)** and rainfall **(b)** measured at the Le Bray site, and Net Ecosystem Exchange (NEE) at Le Bray **(c)**, Bilos **(d)** and La Cape Sud **(e)**, for which we also represent the time change in maize height **(f)**.
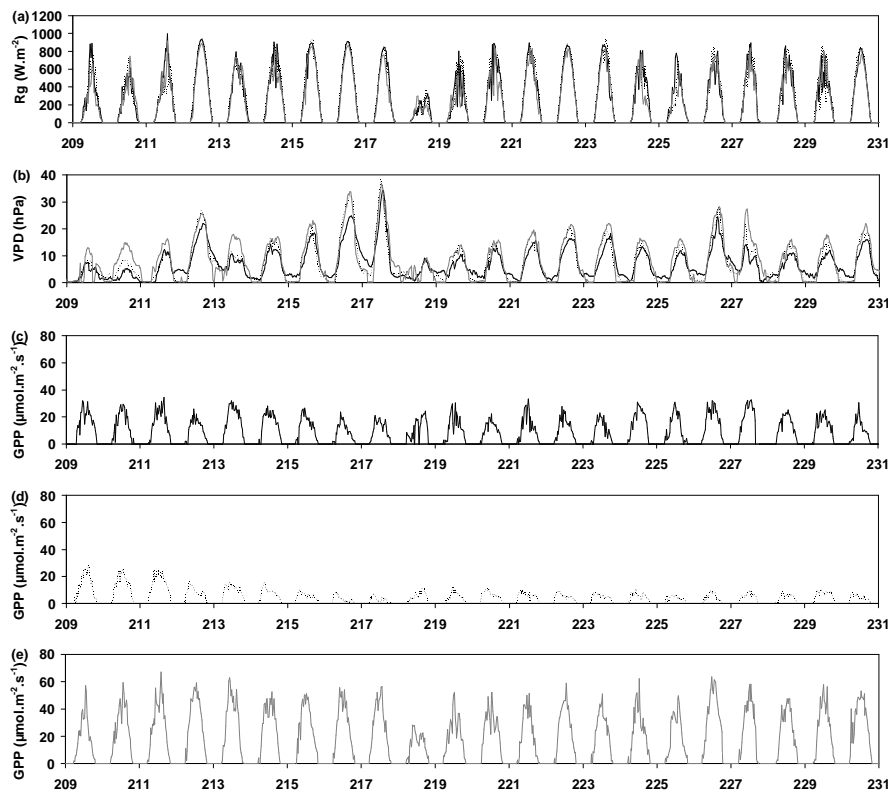
Fig. 2. Time series of global radiation **(a)**, vapour pressure deficit **(b)** and gross primary production (**c** to **e**) for each site from 28 July 2007 (DOY 209) to 18 August 2007 (DOY 230). Note that in (a) and (b), the black lines are for Le Bray, the dotted lines for Bilos and the grey lines for La Cape Sud, as in Fig. (c) to (e).
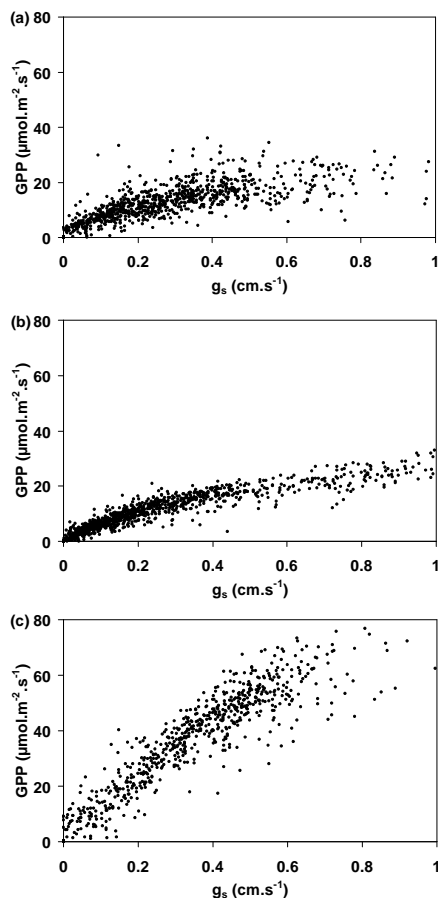
Fig. 3. Gross primary production (GPP) vs. stomatal conductance (g_s) for Le Bray **(a)**, Bilos **(b)** and La Cape Sud during the maturity phase of the maize **(c)**.
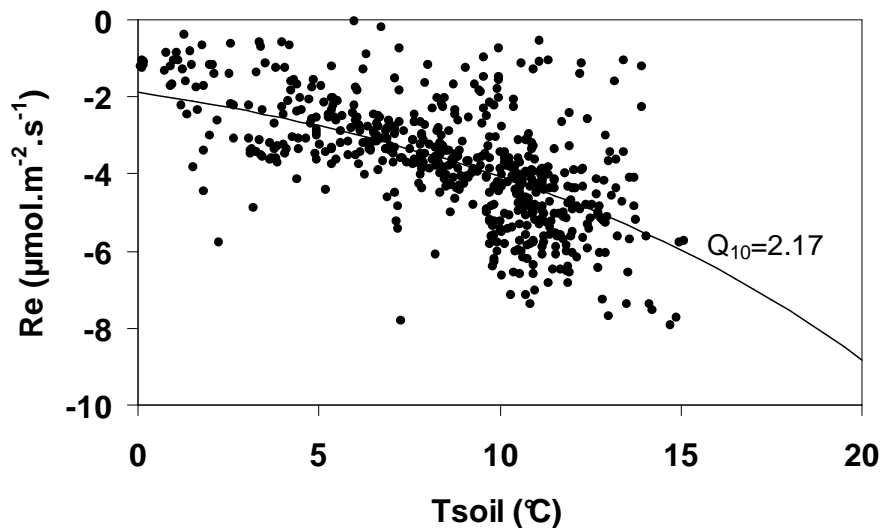
Fig. 4. Relationship between ecosystem respiration (Re) and soil temperature (Tsoil) at La Cape Sud after maize harvest. The dark line represents the Q_{10} function. Only data with $u_* > 0.2 \, \mathrm{m \, s^{-1}}$ are represented and used for the regression.
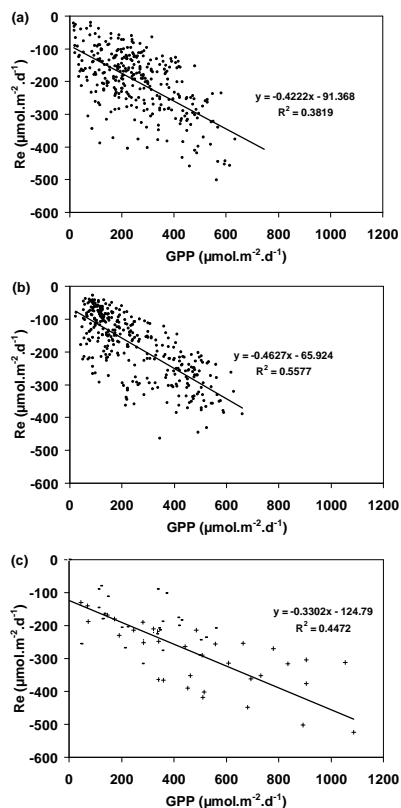
Fig. 5. Daily ecosystem respiration (Re) as a linear function of daily gross primary production (GPP) for Le Bray **(a)**, Bilos **(b)** and La Cape Sud **(c)**. For the two forests (a and b), the data corresponds to the whole period of measurement. For the maize crop (c), the data is restricted to growth (crosses) and senescence (dashes).

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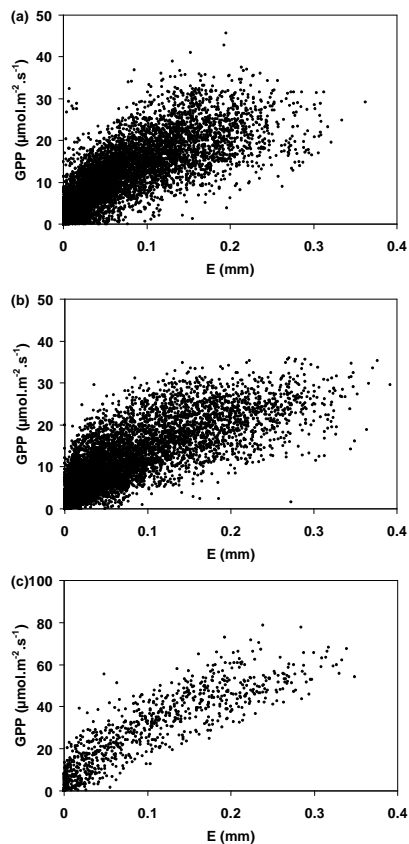
Fig. 6. Relationship between gross primary production (GPP) and water vapour flux (E) for Le Bray **(a)**, Bilos **(b)** and La Cape Sud during the maturity phase of the maize **(c)**. Note that the scale is twice as large for the maize crop.

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Interactive Discussion
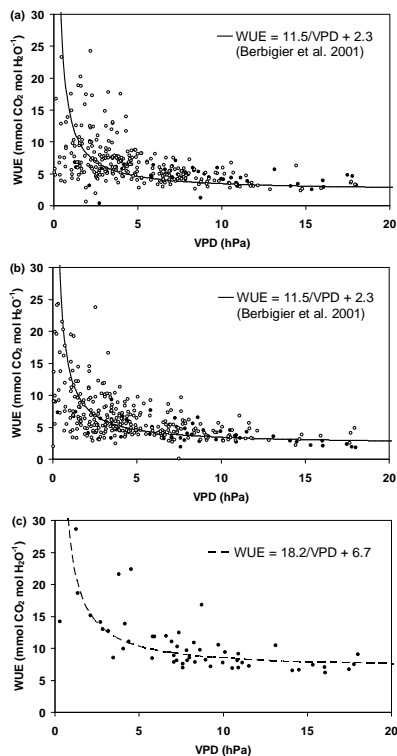
Fig. 7. Daily water use efficiency (WUE) as a function of daily vapour pressure deficit (VPD) for Le Bray **(a)**, Bilos **(b)** and La Cape Sud during the maturity phase of the maize **(c)**. For all sites, filled symbols correspond to data from 11 July to 1 September (period of maturity of the maize 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).

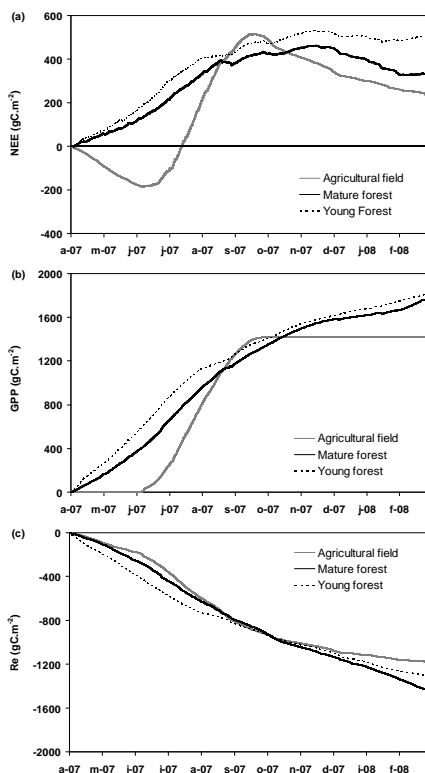Printer-friendly Version

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Fig. 8. (a) Accumulated net ecosystem exchange (NEE), **(b)** accumulated gross primary production (GPP) and **(c)** accumulated ecosystem respiration (Re) for Le Bray (black line), Bilos (dotted line) and La Cape Sud (grey line).