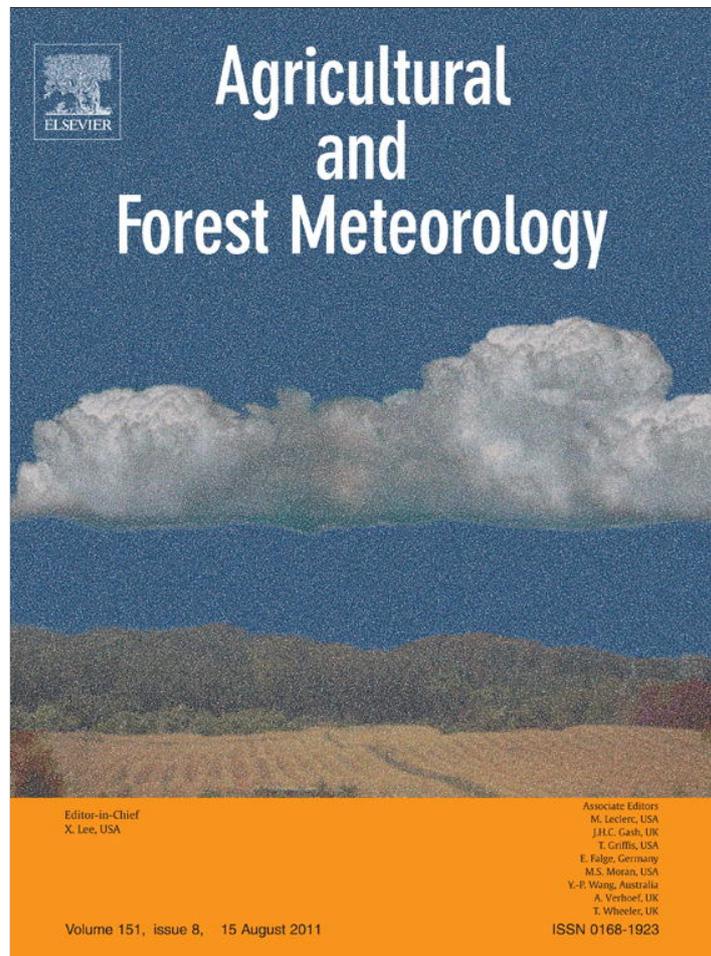


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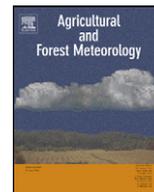
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Agricultural and Forest Meteorology

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Strong seasonal variations in net ecosystem CO₂ exchange of a tropical pasture and afforestation in Panama

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ARTICLE INFO

Article history:

Received 15 November 2010

Received in revised form 31 March 2011

Accepted 4 April 2011

Keywords:

Eddy covariance

Carbon dioxide fluxes

Soil respiration

Land use

ENSO

FLUXNET

ABSTRACT

Pasture and afforestation are land-use types of major importance in the tropics, yet, most flux tower studies have been conducted in mature tropical forests. As deforestation in the tropics is expected to continue, it is critical to improve our understanding of alternative land-use types, and the impact of interactions between land use and climate on ecosystem carbon dynamics. Thus, we measured net ecosystem CO₂ fluxes of a pasture and an adjacent tropical afforestation (native tree species plantation) in Sardinilla, Panama from 2007 to 2009. The objectives of our paired site study were: (1) to assess seasonal and inter-annual variations in net ecosystem CO₂ exchange (NEE) of pasture and afforestation, (2) to identify the environmental controls of net ecosystem CO₂ fluxes, and (3) to constrain eddy covariance derived total ecosystem respiration (TER) with chamber-based soil respiration (R_{Soil}) measurements. We observed distinct seasonal variations in NEE that were more pronounced in the pasture compared to the afforestation, reflecting changes in plant and microbial activities. The land conversion from pasture to afforestation increased the potential for carbon uptake by trees vs. grasses throughout most of the year. R_{Soil} contributed about 50% to TER, with only small differences between ecosystems or seasons. Radiation and soil moisture were the main environmental controls of CO₂ fluxes while temperature had no effect on NEE. The pasture ecosystem was more strongly affected by soil water limitations during the dry season, probably due to the shallower root system of grasses compared to trees. Thus, it seems likely that predicted increases in precipitation variability will impact seasonal variations of CO₂ fluxes in Central Panama, in particular of pasture ecosystems.

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1. Introduction

Tropical ecosystems play an important role in the global carbon cycle. They store 40% of the carbon in the terrestrial biosphere and are responsible for half of the global terrestrial gross primary production (Fisher et al., 2009; Grace et al., 2001). Climate model projections for tropical areas like Amazonia and Central America suggest rising temperatures, a reduction in the total amount of precipitation, and an increase in precipitation variability with more frequent extreme dry seasons by the end of this century (Bates et al., 2008; IPCC, 2007). A recent study by Phillips et al. (2009) suggests a large sensitivity of Amazonian ecosystems to drought, which is contrary to findings of Schwalm et al. (2010) who found only a minimal drought sensitivity of CO₂ fluxes in tropical regions. On the other hand, it is well known that variations of precipitation patterns are strongly associated with ENSO (El Niño Southern Oscil-

lation) events, e.g. in Central Panama (Graham et al., 2006; Lachniet, 2009), but little is known on the impacts of these variations on ecosystem carbon fluxes.

Thus, an improved understanding of tropical ecosystem responses to changing environmental conditions such as more severe seasonal droughts and increased precipitation variability is needed.

The eddy covariance technique (EC) is the established method to directly measure turbulent fluxes of trace gases between the biosphere and the atmosphere (Aubinet et al., 2000; Baldocchi, 2003, 2008). As of March 2010, 502 sites were listed in FLUXNET, the global network of eddy covariance flux tower measurements (www.fluxnet.ornl.gov), which includes a broad range of vegetation types, climates and disturbance regimes (Baldocchi, 2008). However, the distribution of these sites is still largely dominated by temperate climates on the Northern hemisphere, especially within Europe and North America, which was already noted a decade ago (Buchmann and Schulze, 1999). Tropical sites represent only 10% of all sites, and about half of these are located in Brazil. While mature forests dominate these tropical sites in the Amazon region

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(23 FLUXNET sites; e.g. Chambers et al., 2004; da Rocha et al., 2004; Goulden et al., 2004; Hutyyra et al., 2007; Malhi et al., 1998; Priante-Filho et al., 2004; Saleska et al., 2003; Vourlitis et al., 2001), only a few tropical grasslands were studied using the eddy covariance method (4 FLUXNET sites; Sakai et al., 2004; Santos et al., 2004; von Randow et al., 2004). This is surprising since in Central America and the Caribbean, grasslands (including savanna and shrubland) cover approximately 41% of the total land area, making grasslands the most important land-cover along with forests (34%; EarthTrends, 2003).

With ongoing deforestation and related land-use changes, the tropics are increasingly influenced by agroecosystems and pastures. Land-use change is one of the most important contributors to globally increasing CO₂ concentrations, particularly in developing countries (IPCC, 2007) where deforestation is primarily driven by the demand for timber, arable land and livestock production. Following deforestation of native primary forest, the land is typically used to cultivate agricultural crops for a few years, before being converted into grasslands used for grazing (Amézquita et al., 2008). However, only few of these often extensively used grasslands (Malmer et al., 2010) are later considered for afforestation. So far, afforestations (forest plantations), typically with non-native, fast growing or high value timber monocultures like *Eucalyptus*, *Pinus* or *Tectona* (Kanowski, 1997), cover only a minimal area in the tropics. Only 3% are reported for Brazil (FAO, 2001) and 1.6% for Central America and the Caribbean (EarthTrends, 2003), although afforestations are considered an effective measure to sequester carbon and mitigate the anthropogenic induced increasing CO₂ concentrations (FAO, 2009), with a mitigation potential in the order of 15% of global CO₂ emissions (Malhi et al., 2002). However, our knowledge about the carbon cycling of tropical pastures and afforestations including the land-use change in between is very limited. Large uncertainties exist in particular about the sensitivity of newly established ecosystems to changes in environmental conditions (Gilmanov et al., 2010).

Thus, we quantified and compared the net ecosystem CO₂ exchange (NEE) of a traditionally grazed pasture and an adjacent afforestation planted with native tree species. The objectives of our paired-sites study were: (1) to assess seasonal and inter-annual variations in NEE of a pasture and an afforestation in Panama, (2) to identify the environmental controls of net ecosystem CO₂ fluxes, and (3) to constrain eddy covariance derived total ecosystem respiration (TER) with chamber based soil respiration (R_{Soil}) measurements.

We hypothesised that the afforestation with native tree species would be more adapted to the pronounced seasonal climate and therefore be less sensitive to variations in climate. We expected soil moisture (dry season limitations) and radiation (wet season limitations) to be the main environmental controls for NEE. Night-time ecosystem and soil respiration were expected to be controlled by soil moisture and temperature.

2. Materials and methods

2.1. Site description

The Sardinilla site is located in Central Panama (9°19'N, 79°38'W), about 40 km north of Panama City and 30 km north-east of Barro Colorado Island (BCI), at about 70 m a.s.l. The site has a semi-humid tropical climate with a mean annual temperature of 25.2 °C, 2289 mm mean annual precipitation (2007–2009) and a pronounced dry season from January to April characterized by strong North-easterly trade winds (Table 1). Dry season length in Central Panama varies among years (134 ± 19 days for 1954–2009; ACP, 2010) and is influenced by ENSO (Graham et al.,

2006; Lachniet, 2009). Geologically, the site belongs to the *Gatuncillo* formation and the bedrock is classified as tertiary limestone containing clayey schist and quartz sandstone (ANAM, 2010). Soils are classified as Ultisols, with isolated Vertisols at the afforestation and Alfisols at the pasture site (Ben Turner, personal communication), characterised by high clay contents (clay 65%, silt 30%, sand 4%; Abraham, 2004). Consequently, strong soil contractions occur and desiccation cracks developed during the dry season (up to 1 m depth, particularly in the afforestation), enhancing bioturbation of organic material (litter) to deeper soil layers. The afforestation had higher topsoil (0–10 cm) organic carbon and nitrogen concentrations compared to the pasture (4.24% vs. 1.72% and 0.36% vs. 0.17%, respectively). C:N ratios of 10 were found in the pasture and of about 12 in the afforestation site (Table 1).

The Sardinilla site was logged in 1952/1953 and used for agriculture for two years, before it was converted into a pasture (Wilsey et al., 2002). In 2001, an afforestation using native tree species only was established at parts of the site (7.5 ha), while traditional grazing continued on the remaining pasture (6.5 ha). Pasture vegetation is dominated by C₄ grasses, consisting of: *Paspalum dilatatum* (C₄, 50–75%), *Rhynchospora nervosa* (sedge, C₃, 25–50%), *Panicum dichotomiflorum* (C₄, 5–25%) and *Sporobolus indicus* (C₄, 1–5%; listed in the order of abundance according to Braun-Blanquet method). The afforestation consists of six native deciduous and semi-deciduous tree species (*Luehea seemanii*, *Cordia alliodora*, *Anacardium excelsum*, *Hura crepitans*, *Cedrela odorata*, *Tabebuia rosea*), with moderately dense understory vegetation (shrubs, grasses and sedges). Trees that are semi-deciduous are losing either part of their foliage or their foliage only for a very short period. In 2008, estimated mean canopy height was about 10 m in the afforestation and 0.09 m in the pasture (Table 1). The afforestation site has an undulating topography with an elevation range of less than 10 m. In contrast, the adjacent pasture is homogeneously flat with an overall slope of less than 2°.

2.2. Instrumentation and data acquisition

Two flux towers using the eddy covariance method were installed in February 2007: one tower in the afforestation, and the second one in the adjacent, grazed pasture. The micrometeorological measurement systems consisted of an open path infrared gas analyzer (IRGA, Li-7500, LI-COR, Lincoln, USA) and a three-dimensional sonic anemometer (CSAT3, Campbell Scientific, Logan, USA). Instruments were installed at a height of 15 m in the afforestation and at 3 m in the pasture site (Table 1). Micrometeorological data acquisition was carried out with an industry grade embedded box computer (Advantech ARK-3381, Taipei, Taiwan), running a Debian based Linux operating system (Knoppix 4.0.2, Knopper.Net, Schmalenberg, Germany). Measurements of environmental variables included air temperature and relative humidity (MP100A, Rotronic, Bassersdorf, Switzerland), incoming shortwave radiation (R_G , CM3, Kipp & Zonen, Delft, The Netherlands), net radiation (R_N ; afforestation: CN1, Middleton Solar, Brunswick, Australia; pasture: Q*7.1, REBS – Radiation and Energy Balance Systems, Seattle, USA), photosynthetic photon flux density (PPFD, PAR Lite, Kipp & Zonen, Delft, The Netherlands), precipitation (10116 rain gauge, TOSS, Potsdam, Germany), soil heat flux at 5 cm depth (HFP01, Hukseflux, Delft, The Netherlands), soil temperature at 5 cm depth (TB107, Markasub, Olten, Switzerland) and volumetric soil water content (SWC) at 5 and 30 cm depth (EC-5, Decagon, Pullman, USA). Flux measurements were conducted at 20 Hz, meteorological measurements at 10 s and stored as half-hourly averages (sums for precipitation) using data loggers: CR23X at the afforestation and CR10X at the pasture site (both Campbell Scientific, Logan, USA). Precipitation and incoming shortwave radiation were measured at one tower location only. With a distance of 600 m between

Table 1

Flux tower site characteristics for the pasture and the afforestation sites at Sardinilla. Values indicate mean \pm standard error for vegetation height and LAI; mean \pm standard deviation for all soil data. LAI data for the wet season are averages for June and July in 2008 and 2009, for the dry season for March to April 2009. LAI data during the phenological transition month in May 2009 were excluded from averaging.

Site	Pasture	Afforestation
Location	9° 18' 50" N, 79° 37' 53" W	9° 19' 5" N, 79° 38' 5" W
Elevation a.s.l. [m]	68	78
Tower height [m]	3	15
Measurement period	21.03.2007–26.01.2010	05.02.2007–01.07.2009
Canopy height [m]	0.09 \pm 0.07	8–12 (2007–2009)
Vegetation	dominated by C ₄ grasses	six native tree species
LAI of canopy		
Dry season	1.2 \pm 0.14	3.0 \pm 0.28
Wet season	2.9 \pm 0.15	5.4 \pm 0.24
Management	grazing, herbicide treatment (annually in May)	selective understory thinning (December 2007 and 2008)
Prevailing wind direction during daytime [°]		
Dry season	41	87
Wet season	38	69
Mean horizontal wind speed during daytime [m s ⁻¹]		
Dry season	193	165
Wet season	0.97 \pm 0.85	1.73 \pm 1.45
Wet season	2.36 \pm 0.87	3.14 \pm 1.42
Wet season	0.88 \pm 0.64	1.38 \pm 1.06
Soil (0–10 cm)		
Type	Alfisols ^b	Ultisols, Vertisols ^a
Texture	Clay	Clay
Clay, silt, sand [%]	58, 36, 6	65, 30, 4 ^a
pH	5.58 \pm 0.29 ^a	5.76 \pm 0.35 ^a
C [%]	1.72 \pm 0.33	4.24 \pm 0.92
N [%]	0.17 \pm 0.04	0.36 \pm 0.08
C:N	10.11 \pm 0.16	11.86 \pm 1.32
d _B [g/cm ³]	0.86 \pm 0.07 ^a	0.58 \pm 0.09 ^a

^a Abraham (2004).

^b Ben Turner (personal communication).

both flux towers, meteorological conditions can be assumed to be very similar. Regular cleaning of sensors and monthly IRGA calibration checks were performed to assure high data quality. Automated remote connections to Switzerland were established using a GSM modem (GPRS GSM Quadband Modem, ConiuGo, Hohen Neuen-dorf, Germany) to provide daily information on system status and data quality. Although GSM reception proved to be weak at Sardinilla, it was sufficient to transfer small quantities of status information. Both towers had landline power supply although short power outages occurred frequently. However, data acquisition was normally not affected by short interruptions as all instrumentation, except the GSM modem, were powered by 12 V batteries (90 Ah, 105D31L, Solite Batteries, Seoul, Korea). Batteries were charged using automatic battery chargers (J512A/0145-37, Schauer, Cincinnati, USA). All data were stored on the box computer's hard disk with daily backups to an external flash card device (ImageMate CF Reader with 8 GB Ultra II Compact Flash card, SanDisk, Milpitas, USA). For security reasons, a fenced enclosure of 8 m \times 8 m (about 2 m high) was installed around the afforestation tower and a barb-wire fence of 3 m \times 3 m around the pasture tower to prevent access by grazing livestock.

2.3. Data processing and corrections

2.3.1. Flux data

Data acquisition of flux measurements was done with the in-house software *sonicreadHS*, following the concept by Eugster and Plüss (2010). Raw data were processed to half-hourly averages with the in-house eddy covariance software *eth-flux* (Mauder et al., 2008; source code for Unix/Linux systems can be obtained from the authors). *Eth-flux* uses a 2D coordinate rotation with 30 min block averaging. Corrections for damping losses (Eugster and Senn, 1995) and density fluctuations (Webb et al., 1980) were applied during post-processing to the half-hourly averaged data. Subsequently, quality filtering was applied to the flux data using the following rejection criteria: (1) Optical sensor contamination (spider eggs, rain) resulting in high window dirtiness of the IRGAs (AGC value).

We used a 10% threshold above the mean AGC background values of the respective IRGA, which were 62.5% for the pasture and 68.75% for the afforestation site. (2) Filtering for stationarity following Foken and Wichura (1996). We excluded fluxes whenever the 30 min average deviated by more than 100% from the corresponding mean of 5 min averages. (3) CO₂ Fluxes outside the range of -50 to $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ were excluded. (4) Statistical outliers outside the ± 3 SD range of a 14 day running mean window were removed. (5) Periods with low turbulence conditions were excluded based on friction velocity (u^*). We determined seasonal and site-dependent u^* -thresholds according to the method by Gu et al. (2005) and Moureaux et al. (2006), which yielded $u^* < 0.04 \text{ m s}^{-1}$ (dry season), $u^* < 0.03 \text{ m s}^{-1}$ (dry–wet transition) and none during the wet season and wet–dry transition periods for the pasture site. For the afforestation site, u^* -thresholds were $u^* < 0.02 \text{ m s}^{-1}$ (dry season), $u^* < 0.01 \text{ m s}^{-1}$ (wet season), $u^* < 0.05 \text{ m s}^{-1}$ (dry–wet transition) and none during the wet–dry transition period. After quality filtering, 54.6% of good to excellent quality data remained for the pasture (64.7% daytime, 43.6% nighttime data) and 47.6% (65.4% daytime, 28.3% nighttime data) for the afforestation site. For all further data analyses only filtered, high quality flagged data were used. In general, no gap filling was applied to the data. The only exception is Table 4, which shows seasonal sums using the gap filling method by Moffat (unpublished) for daytime and a 10-day running mean approach for nighttime data (Wolf et al., in revision).

Footprint analysis was done using the model by Kljun et al. (2004), which employs a parameterisation based on a scaling procedure over a range of stratifications and which accounts for the influence of roughness length. To aggregate the 30 min footprint information, we generated probability density functions in a polar coordinate grid with 3° per wind direction sector and 5 m distance intervals. All data of the specific seasons were used for footprint analysis.

2.3.2. Meteorological data

Raw meteorological data were quality filtered to eliminate unrealistic measurements and outliers. For periods of instrument

failure, air temperature was derived from virtual temperature measurements of the sonic anemometer based on regression analysis. Due to several instrument failures of PPFd measurements at both tower sites, a joint PPFd variable was derived by regression analysis with incoming shortwave radiation. For times of instrument failure of the rain gauge at the pasture site, data were substituted by those from the nearby (about 5 km to the northeast) Salamanca station of the Panama Canal Authority (ACP; STRI, 2010). When SWC data at 5 cm depth in the pasture were not available, we used SWC data from the afforestation site instead.

2.4. Separation of seasons

Separation of seasons in the semi-humid tropics is generally done based on monthly precipitation sums using a threshold of 100 mm (Hutyra et al., 2007; Loescher et al., 2003; Malhi et al., 2002; Saleska et al., 2003). More sophisticated approaches include variables like sea surface temperatures, wind velocity and position of the Inter-Tropical Convergence Zone, ITCZ (e.g. method used by Panama Canal Authority, STRI, 2010). However, these data are usually not available for flux tower sites. We aimed at a detailed separation of seasons, including transition periods, based on precipitation and thus applied an approach based on daily precipitation sums: (1) wet season is defined as the time span with periods of less than four consecutive days without rain. If three to four consecutive days without rain occurred, the precipitation in the seven days before this period must have exceeded 20 mm (cumulated sum). The start/end of the first/last period of such consecutive days marked the end/start of the wet season. (2) Dry season is defined as the time of the year with consecutive periods of more than four days without any rain. (3) The dry–wet transition period starts with the first heavy rainfall event (>1 mm) after a period of at least seven days without any rain. It ends with the onset of the wet season. (4) The wet–dry transition starts at the end of the wet season, before the first period of at least three consecutive days without rain and after a period of at least six days of rain within one week. It ends with the start of the first period with more than four consecutive days without rain and less than 5 mm of rain within two weeks. When using only a two season separation (dry vs. wet), the transition periods can be added to the dry season. Our procedure based on daily precipitation sums yielded similar results as the monthly 100 mm threshold but with a much better temporal resolution needed for detailed flux data comparisons. It also agreed well with related environmental variables like SWC using visual diagnostics.

2.5. Auxiliary measurements

Auxiliary measurements included measurements of leaf area index (LAI), soil respiration (R_{Soil}) fluxes as well as soil sampling. Leaf area index (LAI) was measured in campaigns with an LAI-2000 (LI-COR, Lincoln, USA) in July 2008 and weekly to bi-weekly from March to July 2009. At the afforestation, LAI was measured separately for the tree canopy (measured at 1 m above ground) and the total canopy including the understory (measured at ground level). We corrected our LAI measurements at the afforestation for the shading effect of tree stems and branches by subtracting the minimum dry-season value of the tree canopy LAI (DOY 107, 2009; LAI=0.42). No correction for the shading by stalks was applied to the LAI measurements at the pasture. Data from the phenological transition month of May 2009 was excluded for averaging seasonal LAI.

In addition, nighttime R_{Soil} fluxes were measured between sunset and sunrise on a campaign basis weekly to bi-weekly in February/March and May to July 2009. We used a self-made closed static chamber system, consisting of a 52.5 cm × 19.5 cm (14.9 L)

cylindrical shaped chamber connected to a closed path infrared gas analyzer (Li-6262, LI-COR, Lincoln, USA). Air was pulled through a 1.2 m Bev-A-Line tubing (6 mm in diameter) at 0.5 L/min using a diaphragm pump (NMP 830 KNDC B, KNF Neuberger, Baltherswil, Switzerland). Chamber measurements were conducted over a period of 5 min with data being recorded every 2 s using a data logger (Pace XR440, Pace Scientific, Mooresville, USA). PVC collars (pasture: $n = 10$; afforestation: $n = 12$) with 5 cm height and 20 cm diameter were installed 2.5 cm deep into the soil. Vegetation cover was manually removed at least 24 h prior to measurements.

Topsoil (0–10 cm) sampling at the afforestation was done in March 2009 using a cylindrical corer (10 cm long, diameter of 6.8 cm; $n = 22$). At the pasture site, three soil profiles from 0 to 100 cm depth were sampled in January 2010, with 10 cm increments, and additional in 5 cm depth. Topsoil values were derived by averaging the samples from 5 and 10 cm depth. Samples were dried for at least 72 h in a drying room at 60 °C, then ground and analyzed for C and N with an elemental analyzer (Thermo Flash 1112 Soil Analyzer, Thermo Fisher Scientific, Waltham, USA) at the Smithsonian Tropical Research Institute (STRI) in Panama.

2.6. Energy balance closure

Based on the first law of thermodynamics, the energy budget at the earth's surface is calculated as the sum of available energy, i.e., the sum of net radiation (R_N) and ground heat flux (Q_G) or the sum of turbulent fluxes of sensible (Q_H) and latent heat (Q_E). Theoretically, both sums should yield equal results. In reality, however, a residual energy balance closure (EBC) term is found if all four components are measured separately:

$$\text{EBC} = \frac{Q_H + Q_E}{R_N - Q_G} \quad (1)$$

The EBC is used as an independent measure to evaluate the performance of eddy covariance flux measurements (Aubinet et al., 2000; Wilson et al., 2002). We derived Q_G from the mean of two soil heat flux plates and corrected for heat storage in the soil layer above according to Monteith and Unsworth (1990). Turbulent fluxes were quality filtered to be within the range of -200 to 800 W m^{-2} and EBC was only calculated for periods when data for all components were available.

2.7. Statistical analyses and general conventions

All statistical analyses were carried out using the statistics software package R, version 2.10.0 (R Development Core Team 2009, www.r-project.org). Daytime data were defined as PPFd > $5 \mu\text{mol m}^{-2} \text{ s}^{-1}$. The terms 'midday' and 'nighttime' were defined as 11:00–13:00 and 0:00–4:00 (UTC), respectively. Negative CO_2 fluxes denote assimilation (carbon uptake) by the ecosystem; positive fluxes indicate respiration (carbon loss). In general, only seasons with full data coverage were used for data analysis. When writing 'seasonal drought', we refer to the plant physiological effects of soil moisture deficiency during the dry season. If not denoted otherwise, a two-sided, unpaired t -test was used to test for statistical differences of means between and within study sites and seasons. Differences in seasonal and diurnal variations were tested using a two-sided F -test.

To assess the normalized relation between seasonal mean midday assimilation ($\text{NEE}_{\text{Midday}}$) and mean nighttime respiration fluxes ($\text{NEE}_{\text{Night}}$), we defined a Midday-Night ratio (MNR)

$$\text{MNR} = \left| \frac{\text{NEE}_{\text{Midday}}}{\text{NEE}_{\text{Night}}} \right| \quad (2)$$

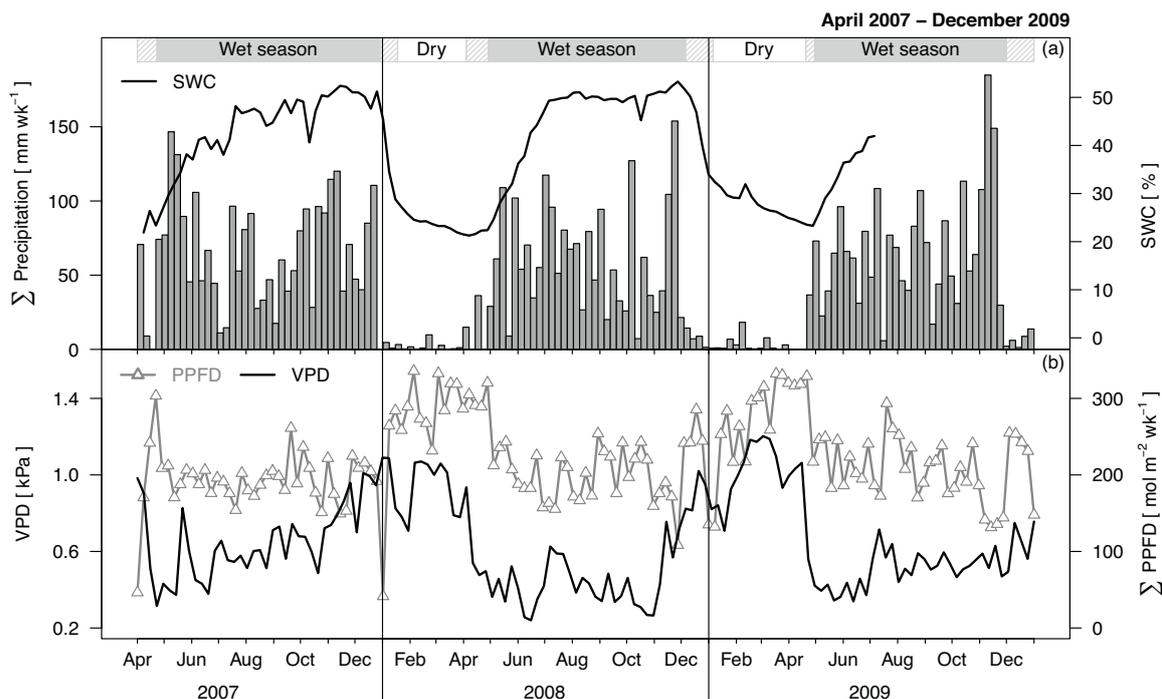


Fig. 1. Weekly precipitation (grey bars) at the Sardinilla pasture and weekly mean volumetric soil water content (SWC; at 5 cm depth) at the Sardinilla afforestation (a). No SWC data were available after June 2009. Weekly mean vapour pressure deficit (VPD) and weekly total photosynthetic photon flux density (PPFD); (b) the inserts at the top indicate the different seasons (wet, dry) including transition periods (shaded areas).

The larger the MNR, the less CO₂ is respired during nighttime in relation to CO₂ being assimilated during midday. An MNR below 1 indicates more CO₂ being respired during nighttime than assimilated during midday, while a MNR of 1 denotes an equal magnitude of these opposing CO₂ fluxes.

3. Results

3.1. Seasonality in climate

We found a pronounced seasonal climate influenced by precipitation in Sardinilla, with a long wet season from May until December, a dry season from January until April, and transition periods with varying and limited amounts of precipitation. Most of the annual precipitation (>98%) was received from April to December (Fig. 1, Table 2). During an average wet season, most precipitation occurred in November (>300 mm), least precipita-

tion in September (about 200 mm). Compared to the long-term annual precipitation mean of the nearby ACP station Salamanca of 2267 mm (1972–2009, derived from STRI, 2010), Sardinilla received above average rainfall in 2007 (2553 mm, +13%), below average rainfall in 2008 (2074 mm, –9%) and about average rainfall in 2009 (2233 mm, –1%). Based on the daily sum of precipitation (seasonal average), less rainfall was observed in the wet season and dry–wet transition period in 2008 compared to 2007 and 2009 (Table 2), while above average rainfall occurred during the wet–dry transition period in 2008. In 2009, the dry season was notably longer (104 days) compared to 2008 (77 days).

Mean soil water content (SWC) at 5 cm depth was closely related to monthly precipitation ($R^2 = 0.40$, $p < 0.001$) and increased swiftly with onset of the wet season (Fig. 1, Table 2). SWC decreased rapidly after the end of the wet season and was lowest during the dry–wet transition period (22%). In 2009, SWC declined less during the dry season compared to 2008. Mean photosynthetic photon

Table 2

Season lengths and climatic conditions at Sardinilla, Panama from 2007 to 2009. Season length (d), seasonal precipitation sum (P), daily precipitation sum (Daily P), mean air temperature (T_{Air}), mean photosynthetic photon flux density (PPFD), mean volumetric soil water content at 5 cm depth (SWC). Meteorological variables reported were measured at the pasture site, except for SWC (afforestation).

	Dates	Length [d]	ΣP [mm]	Daily P [mm d ⁻¹]	Mean T_{Air} [°C]	Mean PPFD [$\mu\text{mol m}^{-2} \text{s}^{-1}$]	SWC [%]
2007	Dry season	until 29.03 ^a	20 ^a	–	25.4 ^a	455 ^a	–
	Dry–wet transition	30.03–22.04	24	82	3.4	26.2	24
	Wet season	23.04–28.12	250	2471	9.9	25.2	45
	Wet–dry transition	29.12–17.01	20	17	0.9	24.9	33
2008	Dry season	18.01–03.04	77	17	0.2	24.7	24
	Dry–wet transition	04.04–28.04	25	51	2.0	25.6	22
	Wet season	29.04–05.12	221	1964	8.9	25.0	46
	Wet–dry transition	06.12–05.01	31	34	1.1	25.1	43
2009	Dry season	06.01–19.04	104	42	0.4	25.1	27
	Dry–wet transition	20.04–29.04	10	37	3.7	26.5	24
	Wet season	30.04–30.11	215	2122	9.9	25.6	35 ^a
	Wet–dry transition	01.12–03.01	34	32	0.9	25.4	–

^a Incomplete, only partial data coverage.

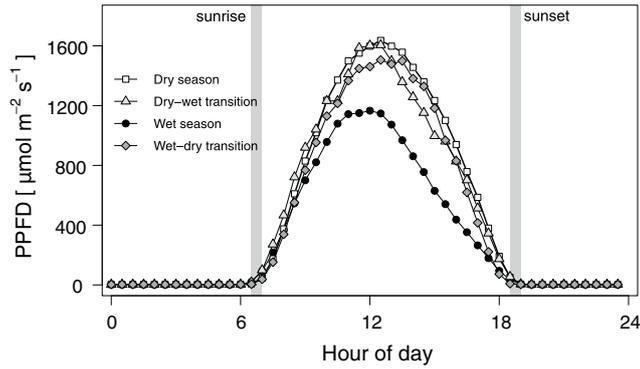


Fig. 2. Diurnal cycles of seasonally averaged photosynthetic photon flux density (PPFD) at Sardinilla from 2007 to 2009. Grey bars denote the seasonally varying times of sunrise and sunset.

flux density (PPFD) varied between $319 \mu\text{mol m}^{-2} \text{s}^{-1}$ during the wet season (max. $1161 \mu\text{mol m}^{-2} \text{s}^{-1}$) and $488 \mu\text{mol m}^{-2} \text{s}^{-1}$ during the dry season, with maximum PPFD of $1636 \mu\text{mol m}^{-2} \text{s}^{-1}$ around noon during the dry season, and $1161 \mu\text{mol m}^{-2} \text{s}^{-1}$ during the wet season (Table 2, Fig. 2). Also the vapour pressure deficit (VPD) showed a pronounced seasonal course with maximum values of up to 1.2 kPa in the dry season (February/March) and minimum values of 0.24 kPa in the wet season. VPD closely followed the diurnal patterns of PPFD (Figs. 2 and 3). Midday VPD was significantly higher at the pasture compared to the afforestation site during the dry and wet season (both $p < 0.01$). Maximum VPD in the dry season 2009 was about 20% higher than in 2008.

Seasonal temperature variations were within $\pm 1^\circ\text{C}$ of the annual mean of 25.2°C at Sardinilla (2007–2009), with a minimum of 24.9°C during the dry season and a maximum of 26.1°C during the dry–wet transition period (Table 2).

3.2. Seasonal variations of NEE

Large seasonal variations of weekly mean midday NEE were observed in Sardinilla that were more prominent in the pasture than in the afforestation (Fig. 4; F -test, $p < 0.001$). We found significantly stronger midday carbon uptake during the wet compared to the dry season at both sites (F -test; pasture $p < 0.001$, afforestation $p < 0.05$). At the pasture site, NEE became positive (respiration dominated) at the end of the dry season and during the dry–wet transition period (up to $5.6 \mu\text{mol m}^{-2} \text{s}^{-1}$). Maximum midday carbon uptake was observed during the middle and at the end of the wet season ($-24.5 \mu\text{mol m}^{-2} \text{s}^{-1}$). The afforestation site maintained carbon uptake throughout all seasons and the highest NEE was found during the dry–wet transition period ($-3.3 \mu\text{mol m}^{-2} \text{s}^{-1}$). During the wet season, similar carbon uptake to the pasture was observed at the afforestation site.

Mean cumulative seasonal NEE indicates carbon losses at the pasture while carbon is sequestered by the afforestation ecosystem throughout most of the year (Table 4).

3.3. Diurnal variations of NEE

3.3.1. Pasture

The pasture ecosystem showed the smallest diurnal variations of NEE during the dry–wet transition period (mean diurnal range of $1.5 \mu\text{mol m}^{-2} \text{s}^{-1}$), with a midday NEE of $0.8 \pm 0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$

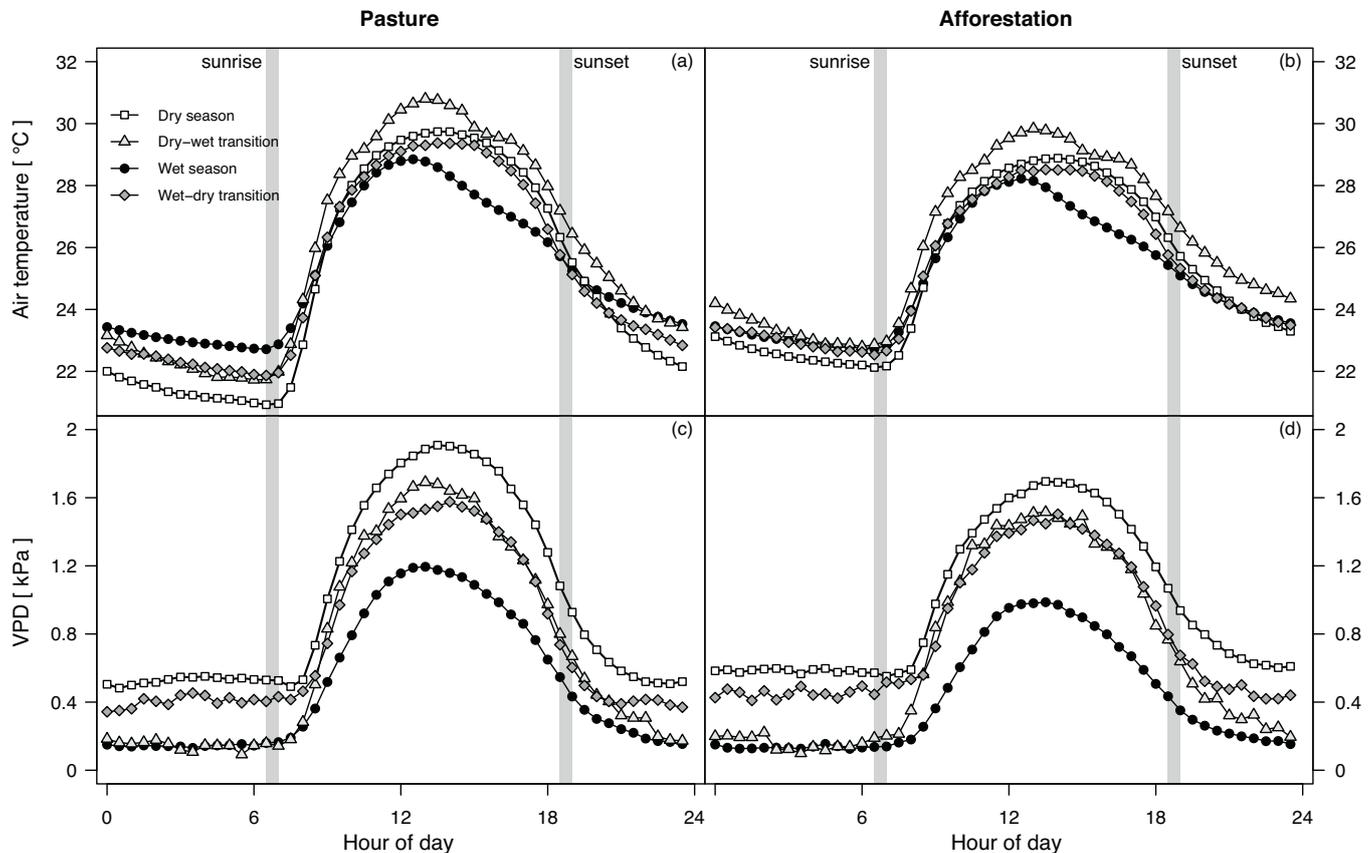


Fig. 3. Diurnal cycles of seasonally averaged air temperature (a and b) and vapour pressure deficit (VPD; c and d) at the Sardinilla pasture and afforestation sites from 2007 to 2009. Grey bars denote the seasonally varying times of sunrise and sunset.

Table 3

Seasonal averages of midday (11:00–13:00) and nighttime (0:00–4:00) net ecosystem CO₂ exchange (NEE; $\mu\text{mol m}^{-2} \text{s}^{-1}$) as well as Midday-Night ratio (MNR) measured over pasture and afforestation in Panama from 2007 to 2009.

	Dry season	Dry-wet transition	Wet season	Wet-dry transition	Total
Pasture					
Midday	-4.4 ± 0.2	0.8 ± 0.5	-16.7 ± 0.6	-18.4 ± 1.0	-13.0 ± 0.4
Nighttime	4.2 ± 0.7	2.3 ± 1.1	7.1 ± 0.5	8.7 ± 1.1	6.5 ± 0.4
MNR	1.0	0.3	2.4	2.1	2.0
Afforestation					
Midday	-8.5 ± 0.3	-5.7 ± 0.8	-15.0 ± 0.6	-10.1 ± 0.1	-12.0 ± 0.4
Nighttime	2.8 ± 0.3	4.0 ± 1.4	5.9 ± 0.5	4.7 ± 1.5	4.7 ± 0.4
MNR	3.0	1.4	2.5	2.1	2.6

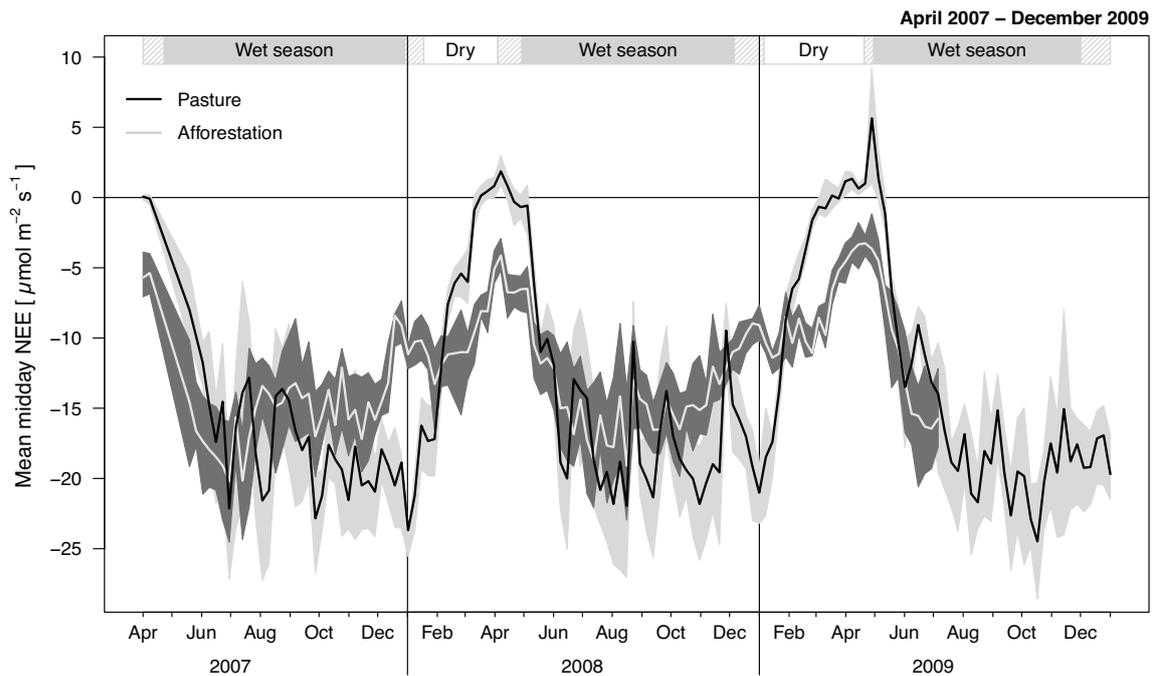


Fig. 4. Inter-annual and seasonal variations of weekly mean midday (11:00–13:00) net ecosystem CO₂ exchange (NEE) at the Sardinilla pasture and afforestation sites. The shaded areas denote the interquartile ranges. The inserts at the top indicate the different seasons (wet, dry) including transition periods (shaded areas). Measurements at the afforestation were discontinued after June 2009.

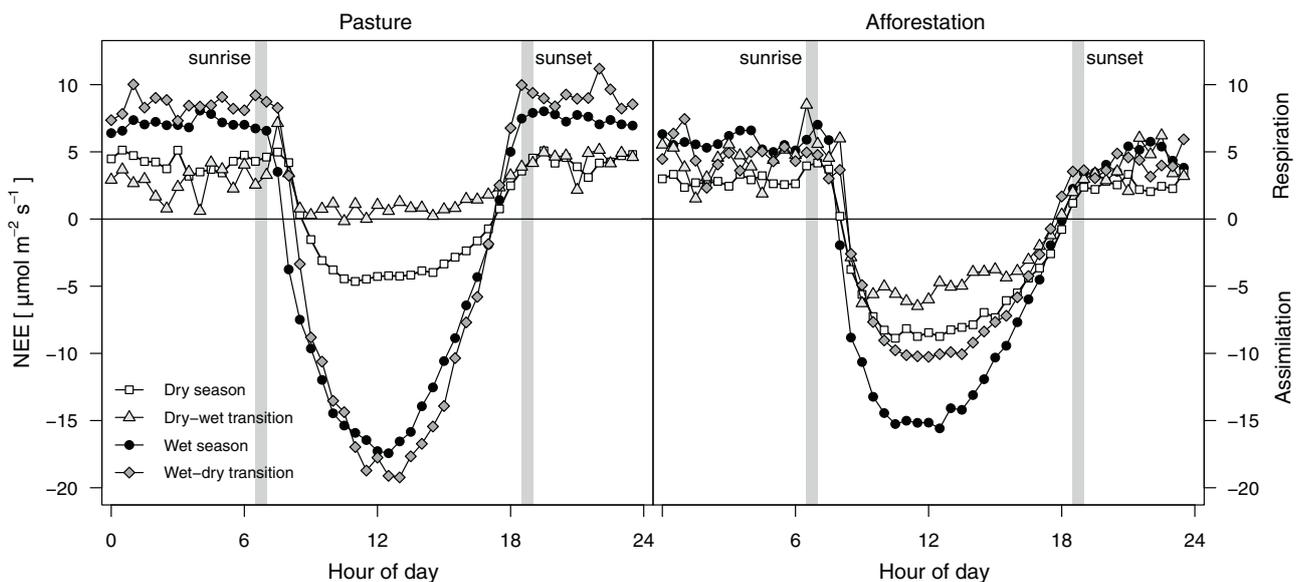


Fig. 5. Diurnal cycles of seasonally averaged net ecosystem CO₂ exchange (NEE) at the Sardinilla pasture and afforestation sites from 2007 to 2009. Grey bars denote the seasonally varying times of sunrise and sunset.

and $2.3 \pm 1.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ during nighttime (Table 3, Fig. 5). These CO_2 losses throughout the day were caused by the mostly senescent pasture vegetation. During the dry season, variations in the diurnal cycle of NEE were still small ($8.6 \mu\text{mol m}^{-2} \text{s}^{-1}$). The largest diurnal variations of NEE were observed during the wet–dry transition period ($27.5 \mu\text{mol m}^{-2} \text{s}^{-1}$), with midday NEE of $-18.4 \pm 1.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $8.7 \pm 1.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ during nighttime.

3.3.2. Afforestation

Similar to the pasture, the afforestation ecosystem also had strongly reduced diurnal variations of NEE during the dry–wet transition period (mean diurnal range of $9.7 \mu\text{mol m}^{-2} \text{s}^{-1}$), with midday NEE of $-5.7 \pm 0.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $4.0 \pm 1.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ during nighttime (Table 3, Fig. 5). During the dry season, NEE was significantly lower during midday ($-8.5 \pm 0.3 \mu\text{mol m}^{-2} \text{s}^{-1}$) and nighttime ($2.8 \pm 0.3 \mu\text{mol m}^{-2} \text{s}^{-1}$) compared to the dry–wet transition period (both $p < 0.001$). During the wet–dry transition period, we observed a midday NEE of $-10.1 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ while NEE at nighttime was comparable to the dry–wet transition period (range of $14.8 \mu\text{mol m}^{-2} \text{s}^{-1}$). The largest diurnal variations of NEE in the afforestation occurred during the wet season ($20.9 \mu\text{mol m}^{-2} \text{s}^{-1}$). Significant differences in diurnal variations of NEE between pasture and afforestation were found during the transition periods only (*F*-test, both $p < 0.001$).

3.3.3. Midday versus nighttime

The ratio of midday assimilation to nighttime respiration (MNR) was constantly larger than 2 in the pasture ecosystem during the wet season and wet–dry transition period (Table 3). However, the MNR was much lower during periods with water limitations: During the dry season, NEE during midday and nighttime were in the same order of magnitude in the pasture ecosystem (MNR = 1), while respiration exceeded assimilation even at daytime during the dry–wet transition period (MNR = 0.3). At the afforestation site, similar ratios to the pasture were found during the wet season and wet–dry transition period (Table 3). Opposing patterns were found during the dry season and dry–wet transition period: NEE at midday exceeded NEE during nighttime significantly in the dry season (MNR = 3.0) and NEE at midday was still higher than at nighttime during the dry–wet transition period (MNR = 1.4).

3.4. Nighttime soil and ecosystem respiration

Mean nighttime R_{Soil} at the pasture site was $1.4 \pm 0.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ during the dry season and decreased to a minimum of $0.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ in March 2009 (Fig. 6). During the wet season, mean R_{Soil} at the pasture was significantly higher ($3.7 \pm 0.8 \mu\text{mol m}^{-2} \text{s}^{-1}$; $p < 0.001$) compared to the dry season and increased to a maximum of $4.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ in June 2009. EC measured nighttime TER was consistently higher than R_{Soil} , with $3.5 \pm 1.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $7.0 \pm 1.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ for dry and wet season, respectively (both $p < 0.001$). At the afforestation site, we observed similar R_{Soil} to the pasture during the dry season ($1.4 \pm 0.2 \mu\text{mol m}^{-2} \text{s}^{-1}$), except for a higher minimum rate (Fig. 6, $1.1 \mu\text{mol m}^{-2} \text{s}^{-1}$). During the wet season, R_{Soil} at the afforestation was lower ($3.2 \pm 0.7 \mu\text{mol m}^{-2} \text{s}^{-1}$; maximum $4.2 \mu\text{mol m}^{-2} \text{s}^{-1}$) but not statistically different from that of the pasture site. Mean TER at the afforestation was also lower during the dry ($3.3 \pm 1.1 \mu\text{mol m}^{-2} \text{s}^{-1}$) compared to the wet season ($5.9 \pm 1.5 \mu\text{mol m}^{-2} \text{s}^{-1}$; $p < 0.001$).

No significant differences in R_{Soil} and TER were found between both sites in Sardinilla. Similar seasonal patterns were observed with only small differences between the sites: the fraction of R_{Soil} contributing to TER was smaller during the dry (40 and 42%) than

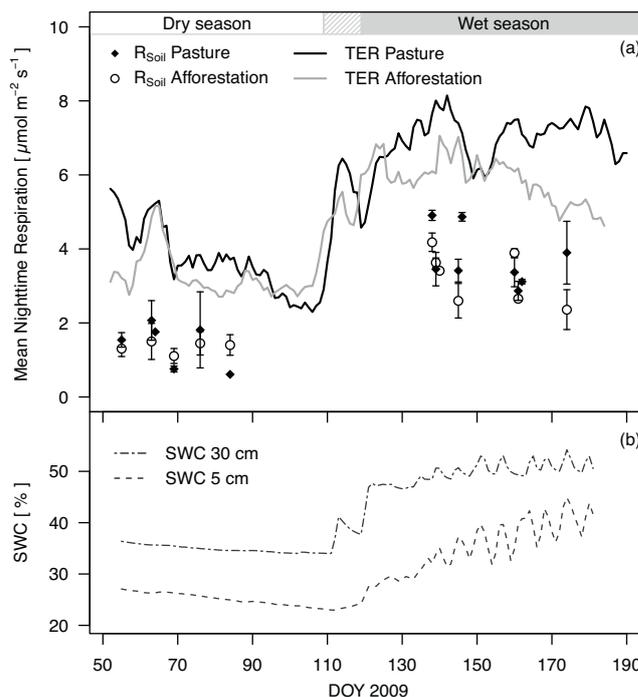


Fig. 6. Mean nighttime soil respiration (R_{Soil} , based on chamber measurements) and total ecosystem respiration (TER, based on eddy covariance measurements) for the Sardinilla pasture and afforestation sites during February to July 2009 (a). Soil respiration is given as means \pm standard errors. TER is displayed as \pm 3 days running mean. Volumetric soil water content (SWC) at 5 and 30 cm depth was measured at the Sardinilla afforestation site (b).

during the wet season (52 and 54%) for pasture and afforestation, respectively.

3.5. Environmental controls of CO_2 fluxes

3.5.1. Daytime NEE

Radiation and soil moisture were the main environmental controls of daytime NEE in Sardinilla. Half-hourly NEE was well correlated with PPFD at the pasture ($r = -0.58$) and afforestation site ($r = -0.53$), and explained 34% and 28% of the variance in NEE, respectively (regression analysis, both $p < 0.001$; not shown). SWC was the strongest residual predictor for NEE at both sites but with differences in depth: 5 cm depth at the pasture (31%) and 30 cm depth at the afforestation (16%; both $p < 0.001$). VPD was only a minor controlling factor of NEE in Sardinilla and explained 3% of the residuals at the pasture and 4% at the afforestation (both $p < 0.001$). Altogether, the factors PPFD, SWC and VPD explained 66% and 50% of the variations in NEE (forward multiple regression analysis) for pasture and afforestation, respectively (both $p < 0.001$). However, when considering seasonal variations, SWC in 5 cm depth was the dominating environmental control of NEE in Sardinilla, with $R^2 = 0.65$ at the pasture and $R^2 = 0.51$ (both $p < 0.001$) at the afforestation site (Fig. 1, weekly means).

3.5.2. Respiratory fluxes (nighttime)

Variations in R_{Soil} were largely associated with seasonal variations in SWC (Fig. 6). For the pasture site, the functional relationship of R_{Soil} to SWC was strongest at 5 cm depth ($R^2 = 0.27$, $p < 0.001$) while it was strongest at 30 cm depth for the afforestation site ($R^2 = 0.39$; $p < 0.001$). At very high, almost water saturated SWC values, R_{Soil} decreased, probably due to anoxic conditions in the water filled pore space. We found no significant relationship of R_{Soil} with soil temperature (T_{Soil}) at both sites. Similar environmental controls as for R_{Soil} were found for TER, although notably weaker

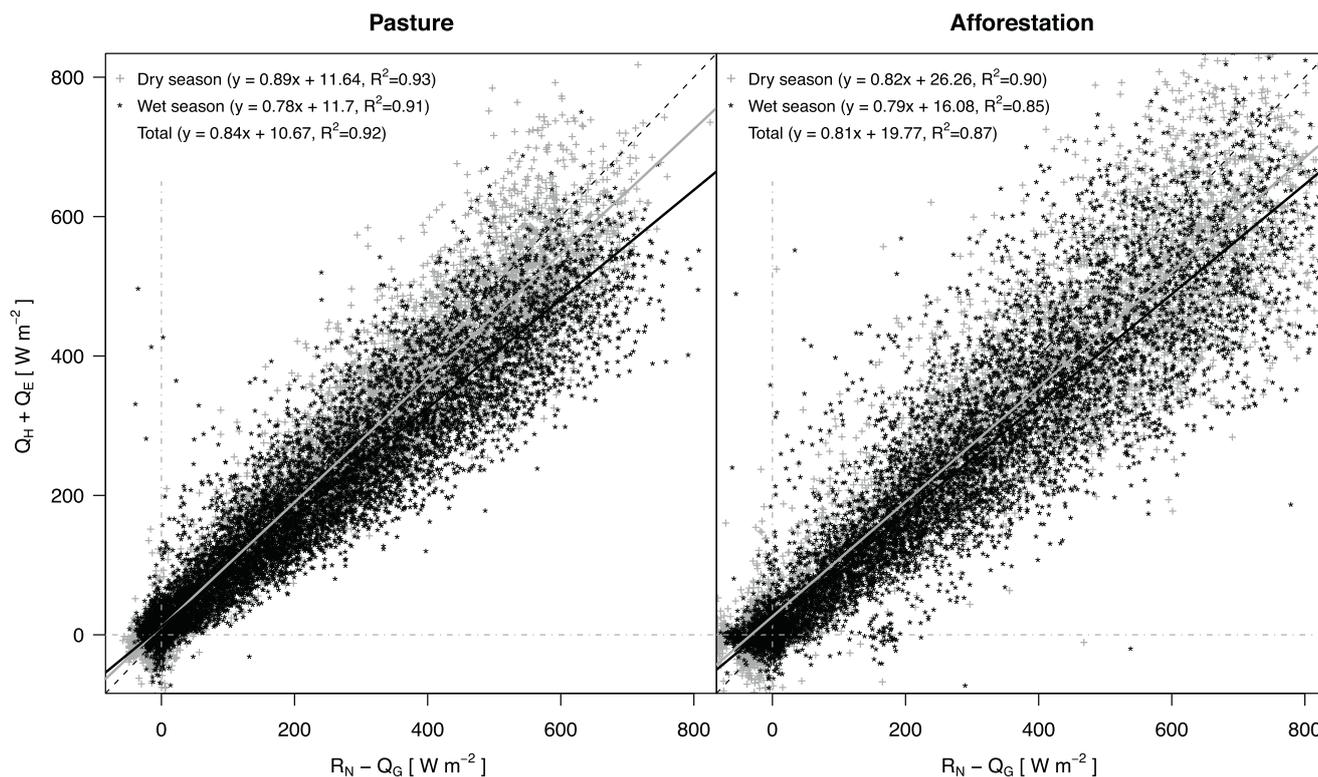


Fig. 7. Seasonal energy balance closure for the Sardinilla pasture and afforestation sites. The grey dashed line denotes the ideal closure (1:1), the grey line is the best fit for the dry season and the black line is the best fit for the wet season. Linear regressions for all seasons are highly significant ($p < 0.001$) for both sites.

for SWC at both sites ($R^2 = 0.03$, $p < 0.001$). We found only a weak temperature sensitivity of TER to soil and air temperature ($R^2 < 0.02$, $p < 0.001$).

3.6. Quality assessment of flux data

3.6.1. Energy balance closure

Assessing energy balance closure (EBC), we found a regression slope of 0.84 and an intercept of 10.8 at the pasture site ($R^2 = 0.92$, $p < 0.001$). Furthermore, pronounced seasonal differences were observed and EBC was better during the dry compared to the wet season (Fig. 7). At the afforestation site, the regression slope of the EBC was 0.81, the intercept 19.73 ($R^2 = 0.87$, $p < 0.001$), and only minor seasonal differences were found. The EBC at the Sardinilla sites are comparable to other flux tower sites globally (Wilson et al., 2002) and underlines the quality of our EC measurements.

3.6.2. Footprint modelling

Footprint estimates at the pasture site extended 70 m into the prevailing wind direction (north-east) and measured CO_2 fluxes were constrained to the pasture area all-season (Fig. 8). At the afforestation site, footprint estimates extended 150–200 m to easterly directions and additionally, to southerly and westerly directions during the wet season. Consequently, measured CO_2 fluxes predominantly originated from within the afforestation area: only a small percentage was contributed from adjacent pasture land during the wet season ($\leq 10\%$) and a slightly higher percentage during the dry season ($\leq 25\%$). Overall, the footprint estimates confirmed that the measured CO_2 fluxes in Sardinilla are representative for the respective land-use type's pasture and afforestation.

3.7. Phenology

At the pasture site, vegetation became senescent during the progressing dry season (mean LAI = 1.2) and LAI declined to a minimum of 0.6 in April 2009 (Table 1, Fig. 9). With the onset of the wet season LAI increased again, reaching a maximum of 3.3 in July (mean LAI = 2.9). The drop of LAI in the pasture in mid June (DOY 168) was caused by an herbicide application in the beginning of June and hence the death of weeds. The afforestation site was characterised by reduced canopy cover during the dry season (mean LAI = 3.0) as most tree species defoliate and understory vegetation became senescent (Table 1, Fig. 9). Bud break occurred within the first weeks of the wet season for most species. Subsequently, canopy cover was increasing rapidly and understory vegetation recovered faster than tree canopy LAI. During the wet season 2009, the afforestation had a fully closed canopy (mean LAI = 5.4) and reached a maximum LAI of 6.0 in July. Overall, LAI was significantly higher at the afforestation compared to the pasture during the dry and wet season (both $p > 0.001$).

4. Discussion

The results support our initial hypothesis that afforestation with native tree species is more adapted to a pronounced seasonal climate in the tropics. This indicates that afforestation compared to pasture will be less affected by projected changes in precipitation patterns (reduction and increased variability) for Central America (Bates et al., 2008). The larger seasonal variations of NEE in pasture compared to afforestation in Sardinilla agree with the results reported by Priante-Filho et al. (2004), while von Randow et al. (2004) reported smaller variations of NEE for pasture compared to forest in Amazonia. As dry season length is similar, non-climatic factors such as species composition or land management could be responsible for such differences.

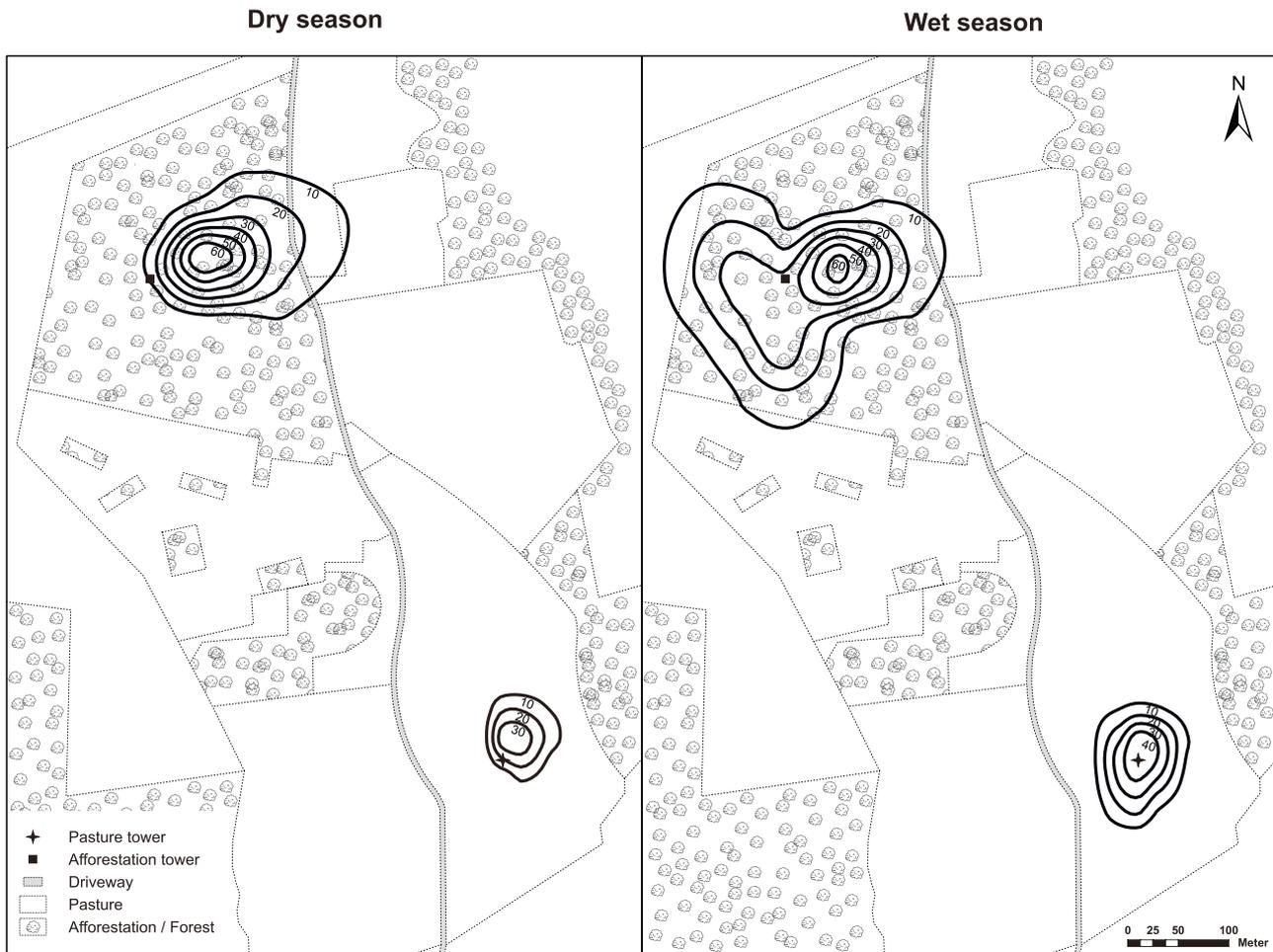


Fig. 8. Footprint estimates of the two Sardinilla sites for dry and wet season using the model by Kljun et al. (2004). Footprint contours (10% intervals) show lines of equal contribution to the statistical mean flux with respect to the grid cell with maximum (100%) contribution.

4.1. Inter-annual precipitation patterns

Our results indicate that it seems likely that ENSO events and associated increases in precipitation variability impacted CO₂ fluxes in Sardinilla during our observations from 2007 to 2009, particularly in the pasture. ENSO events regularly evolve during the period of April to June and reach their maximum strength during December to February (IRI, 2010). During the cold phase of ENSO (La Niña), Central Panama regularly receives higher precipitation, with the months June to August being wet and cool (Graham et al., 2006; IRI, 2010; Lachniet, 2009; NOAA, 2010). Recent La Niña events occurred in 2007 (strong; Trenberth and Fasullo, 2010) and 2008 (weak). Sardinilla received above average rainfall in 2007 and, succeeding this strong La Niña year, experienced a shorter than average dry season in 2008 (Table 2). This pattern is also observed in long-term datasets (ACP, 2010) and reported in the literature (Lachniet, 2009). On the other hand, during the warm phase of ENSO (El Niño), Central Panama regularly receives below average rainfall, with the months June to August being dry and warm. A moderate El Niño occurred in 2009 (fully developed by June 2009), persisting into the beginning of 2010 (IRI, 2010; Trenberth and Fasullo, 2010). Subsequently, the dry season of 2010 started notably early (end of November 2009), which is a pattern frequently observed following El Niño events in Panama (Lachniet, 2009). ENSO events not only affect the amount of precipitation, but also its variability: the El Niño in 2009 resulted in a longer dry season but at the same time, more precipitation occurred (Table 2). As a consequence, soil moisture levels were higher compared to 2008 and we observed

increased CO₂ release from the Sardinilla pasture during the dry season in 2009.

4.2. Daytime NEE

Compared to other tropical pastures, daytime NEE in the Sardinilla pasture (mean $-13 \mu\text{mol m}^{-2} \text{s}^{-1}$) was higher than reported by Santos et al. (2004) from Fazenda Rio de Janeiro (Brazil) during the dry ($-15 \mu\text{mol m}^{-2} \text{s}^{-1}$) and wet season ($-40 \mu\text{mol m}^{-2} \text{s}^{-1}$). In contrast, NEE was lower in Sardinilla compared to a study by Priante-Filho et al. (2004) that observed $-9 \mu\text{mol m}^{-2} \text{s}^{-1}$ in Cotriguacú (Brazil) during the wet season. Overall, these differences to other tropical pastures seem largely related to management factors, like grazing intensity, herbicide application and fertilization (Gilmanov et al., 2010; Wang and Fang, 2009; White et al., 2000). Compared to Sardinilla, the pasture reported by Priante-Filho et al. (2004) was intensively managed (regular burnings and grass cuts, 2nd year of afforestation) and the pasture reported by Santos et al. (2004) was ungrazed.

When comparing our young afforestation with mature tropical forest, daytime NEE in the Sardinilla afforestation ($-12 \mu\text{mol m}^{-2} \text{s}^{-1}$) is in the lower range of tropical forests (-8.3 to $-19 \mu\text{mol m}^{-2} \text{s}^{-1}$): Hutrya et al. (2007) reported a higher mean daytime NEE of $-8.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ and von Randow et al. (2004) observed about similar daytime NEE ($-12.5 \mu\text{mol m}^{-2} \text{s}^{-1}$, mean of dry and wet season) in Amazonia. Contrary to Sardinilla, lower daytime NEE were observed at other tropical forest sites, e.g. as reported by Loescher et al. (2003) from Costa Rica

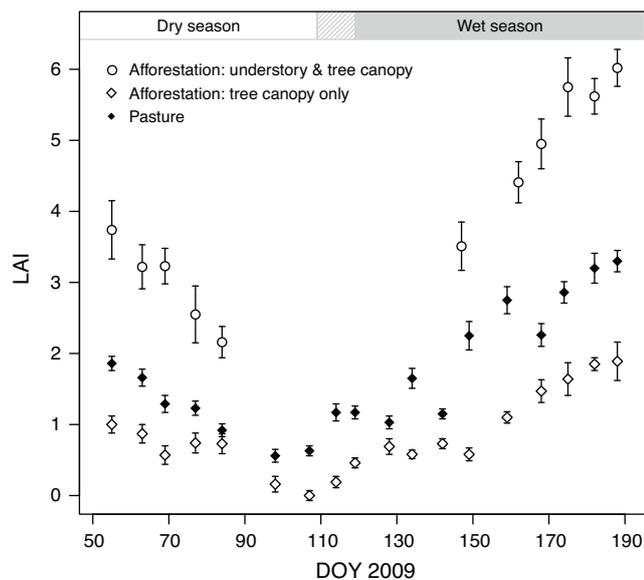


Fig. 9. Leaf area index (LAI) for the Sardinilla pasture and afforestation sites during February to July 2009. Means \pm standard errors are given. No measurements of afforestation understory LAI were taken between DOY 85 and 146.

($-18 \mu\text{mol m}^{-2} \text{s}^{-1}$) or Goulden et al. (2004; $-17.5 \mu\text{mol m}^{-2} \text{s}^{-1}$, derived mean of reported range) and Saleska et al. (2003) from Amazonia ($-15 \mu\text{mol m}^{-2} \text{s}^{-1}$). Overall, the differences in daytime NEE compared to mature tropical forest seem to be related to the young age of the Sardinilla afforestation and likely become smaller with the aging of the trees.

4.3. Controls of CO_2 fluxes

Radiation was the main environmental control of daytime CO_2 fluxes in Sardinilla, supporting our initial expectations. In addition, soil moisture showed a pronounced seasonality and the pasture ecosystem was more affected by seasonal drought than the afforestation. This is probably related to differences in soil water access due to the larger rooting depth of trees (tap roots, access to deeper water sources) versus the shallow roots of grasses (Jackson et al., 1996). von Randow et al. (2004) also reported deep water access and hence, reduced drought sensitivity of forest compared to pasture in South West Amazonia during the dry season. As long as trees still have access to ground water – which is normally the case for native tree vegetation under typical seasonal dryness, explaining their competitive advantage over other non-native vegetation types – trees will remain more productive than pasture at this site. How pasture vegetation will respond to a serious drought is unclear, however, this situation seems not very likely in the near future, given recent IPCC scenarios for Panama.

Besides environmental controls, plant physiological differences between C_3 and C_4 plants affected CO_2 fluxes in Sardinilla: with the more efficient photosynthetic pathway of the dominating C_4 grasses at the pasture (Ehleringer and Monson, 1993), this ecosystem achieved higher midday assimilation rates during the wet season than the afforestation (dominated by C_3 trees).

4.4. Nighttime respiratory fluxes

Our results confirm the expectation that soil moisture is an important environmental control for respiratory fluxes in Sardinilla, similar to observations at other tropical sites (Adachi et al., 2006; Davidson et al., 2000) and for plants with similar ecophysiological characteristics (Vargas et al., 2010). On the other hand,

Table 4

Mean cumulative seasonal net ecosystems exchange (NEE) from gap filled data at the Sardinilla pasture and afforestation sites from 2007 to 2009. Mean annual NEE estimates from all seasons were $253 \text{ gC m}^{-2} \text{ yr}^{-1}$ and $-422 \text{ gC m}^{-2} \text{ yr}^{-1}$ and gap filling accounted for 45.4% and 52.4% of all data for pasture and afforestation, respectively.

	Pasture [gC m^{-2}]	Afforestation [gC m^{-2}]
Dry season	172	-83
Dry-wet transition	64	11
Wet season	10	-337
Wet-dry transition	7	-13

our results contradict the effect of temperature, which is surprising as microbial activity, i.e. heterotrophic soil respiration, typically has a strong temperature dependency. However, temperature variations in Sardinilla were small during nighttime (on average only about 2°C) which seems to explain the relatively low power to find such temperature sensitivity. Similar weak sensitivity was reported from Hutrya et al. (2007) from the Amazon and Davidson et al., 2006 for tropical soils in general.

Compared to other tropical sites, R_{Soil} in the Sardinilla pasture and afforestation were within the range reported for tropical forests (Buchmann et al., 2004). However, the R_{Soil} values in the afforestation were in the lower range compared to other tropical forest sites, probably due to the young age of the afforestation (planted in 2001). At the afforestation site, R_{Soil} during the dry season 2009 was similar to R_{Soil} measured at the same site by Murphy et al. (2008) in 2004 ($1.0 \pm 0.7 \mu\text{mol m}^{-2} \text{ s}^{-1}$). In contrast, R_{Soil} during the wet season 2009 was much lower than the values reported by Murphy et al. (2008), although the variability of the 2004 measurements was an order of magnitude larger ($7.2 \pm 3.5 \mu\text{mol m}^{-2} \text{ s}^{-1}$). These differences are supposedly related to the small size of the trees in 2004 and the associated larger ground cover with C_4 understory vegetation (grasses).

Compared to other tropical pastures, TER observed in the Sardinilla pasture was higher than reported by von Randow et al. (2004) and lower than TER reported by Santos et al. (2004). These differences seem related to grazing, particularly as the latter study was conducted at an ungrazed site with exceptionally high NEE in general (Santos et al., 2004). Priante-Filho et al. (2004) observed comparable TER during the wet season with only small differences between a pasture and forest site. Strong increases in TER at both sites during the dry-wet transition period were closely related to increasing soil moisture and stimulated microbial activity. Large amounts of leaf litter (afforestation) and manure (pasture) accumulated during the dry season, when decomposition was inhibited by moisture limitations (Scherer-Lorenzen et al., 2007). Eventually, the accumulated organic material started to decompose rapidly following the first rainfalls during the dry-wet transition period ('Birch effect') and caused the strong increases in TER.

5. Conclusions

Land-use change has a strong impact on net ecosystem CO_2 fluxes in Central Panama. The pasture studied in Sardinilla is more strongly affected by soil water limitations during the dry season than the afforestation, most likely due to the shallow roots of grasses. Consequently, land-use change from pasture to afforestation can reduce seasonal variations in CO_2 fluxes and the sensitivity to seasonal drought under present day climate conditions. Midday assimilation fluxes are persistently larger than nighttime respiratory fluxes in the afforestation ecosystem, indicating a potential for carbon uptake by the ecosystem throughout most of the year (c.f. Table 4). Future research should focus on the effects of land management on tropical afforestation (e.g. thinning, pruning, harvest) and the effects of grazing intensity on pasture ecosystem CO_2 fluxes. Our results suggest that ENSO events and associated

increases in precipitation variability impact ecosystem fluxes and seasonal variations of CO₂ fluxes in Central Panama, particularly for pasture. However, long-term measurements are needed to constrain these patterns more comprehensively. With projected changes in precipitation patterns for Central America (reduction and increased variability), it can be expected that the variations of CO₂ fluxes in pasture ecosystems will increase. As long as serious droughts are not lowering the ground water table below the reach of tree roots, it can be expected that the afforestation remains more productive than the pasture in Sardinilla, Panama.

Acknowledgements

Funding for this project was provided by the North–South Centre (former Swiss Centre for International Agriculture) of ETH Zurich. We thank the Meteorology and Hydrology Branch of the Panama Canal Authority (ACP), Republic of Panama, for providing meteorological data. We are grateful to Timothy Seipel for identifying grass species of the pasture and for valuable comments on the manuscript. Many thanks also to Nicolas Gruber for inspiring discussions. We particularly thank José Monteza for assistance in the field.

References

- Abraham, M., 2004. Spatial variation in soil organic carbon and stable carbon isotope signature in a pasture and a primary forest in Central Panama. Master thesis Thesis, McGill University, Montreal, 91 pp.
- ACP, 2010. Meteorological Data. Panama Canal Authority (ACP), Meteorology and Hydrology Branch (Republic of Panama), Data provided by Mike Hart.
- Adachi, M., Bekku, Y.S., Rashidah, W., Okuda, T., Koizumi, H., 2006. Differences in soil respiration between different tropical ecosystems. *Applied Soil Ecology* 34 (2–3), 258–265.
- Amézquita, M.C., Murgeitio, E., Ramirez, B.L., Ibrahim, M.A., 2008. Tropical America: land use, land use change, economic and environmental importance of pasture and silvopastoral production systems. In: 't Mannetje, L., Amézquita, M.C., Buurman, P., Ibrahim, M.A. (Eds.), *Carbon Sequestration in Tropical Grassland Ecosystems*. Wageningen Academic Publishers, Wageningen, The Netherlands, p. 221.
- ANAM, 2010. Geological Map of Panama. Autoridad Nacional del Ambiente of Panama (ANAM), <http://mapserver.anam.gob.pa>, 15.01.2010.
- 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., Grunwald, T., Morgenstern, K., Pilegaard, K., Rebmann, C., Snijders, W., Valentini, R., Vesala, T., 2000. Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology. *Advances in Ecological Research*, vol. 30. Academic Press Inc., San Diego, pp. 113–175.
- Baldocchi, D.D., 2003. Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. *Global Change Biology* 9 (4), 479–492.
- Baldocchi, D.D., 2008. Breathing of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. *Australian Journal of Botany* 56 (1), 1–26.
- Bates, B.C., Kundzewicz, Z.W., Wu, S., Palutikof, J.P. (Eds.), 2008. *Climate Change and Water*. Technical Paper of the Intergovernmental Panel on Climate Change. IPCC Secretariat, Geneva, p. 210.
- Buchmann, N., Schulze, E.D., 1999. Net CO₂ and H₂O fluxes of terrestrial ecosystems. *Global Biogeochemical Cycles* 13 (3), 751–760.
- Buchmann, N., Bonal, D., Barigah, T.S., Guehl, J.M., Ehleringer, J.R., 2004. Insights in the carbon dynamics of tropical primary rainforests using stable carbon isotope analyses. In: Gourlet-Fleury, S., Guehl, J.M., Laroussinie, O. (Eds.), *Ecology and Management of a Neotropical Rainforest*. Elsevier, Applied Science, London, NY.
- Chambers, J.Q., Tribuzy, E.S., Toledo, L.C., Crispim, B.F., Higuchi, N., dos Santos, J., Araujo, A.C., Kruijt, B., Nobre, A.D., Trumbore, S.E., 2004. Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency. *Ecological Applications* 14 (4), 72–88.
- da Rocha, H.R., Goulden, M.L., Miller, S.D., Menton, M.C., Pinto, L., de Freitas, H.C., Figueira, A., 2004. Seasonality of water and heat fluxes over a tropical forest in eastern Amazonia. *Ecological Applications* 14 (4), 22–32.
- Davidson, E.A., Verchot, L.V., Cattanio, J.H., Ackerman, I.L., Carvalho, J.E.M., 2000. Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia. *Biogeochemistry* 48 (1), 53–69.
- Davidson, E.A., Janssens, I.A., Luo, Y.Q., 2006. On the variability of respiration in terrestrial ecosystems: moving beyond Q(10). *Global Change Biology* 12 (2), 154–164.
- EarthTrends, 2003. *Forests, Grasslands, and Drylands – Country Profile Panama*. World Resource Institute (11.05.2010) http://earthtrends.wri.org/country-profiles/fetch_profile.php?theme=9&filename=for_cou.591.PDF.
- Ehleringer, J.R., Monson, R.K., 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. *Annual Review of Ecology and Systematics* 24, 411–439.
- Eugster, W., Plüss, P., 2010. A fault-tolerant eddy covariance system for measuring CH₄ fluxes. *Agricultural and Forest Meteorology* 150 (6), 841–851.
- Eugster, W., Senn, W., 1995. A cospectral correction model for measurement of turbulent NO₂ flux. *Boundary-Layer Meteorology* 74 (4), 321–340.
- FAO, 2001. *Global Data on Forest Plantations Resources*. Food and Agriculture Organization of the United Nations (FAO), Rome.
- FAO, 2009. *State of the World's Forests 2009*. Food and Agriculture Organization of the United Nations (FAO), Rome.
- Fisher, J.B., Malhi, Y., Bonal, D., Da Rocha, H.R., De Araujo, A.C., Gamo, M., Goulden, M.L., Hirano, T., Huete, A.R., Kondo, H., Kumagai, T., Loescher, H.W., Miller, S., Nobre, A.D., Nouvellon, Y., Oberbauer, S.F., Panuthai, S., Rouspard, O., Saleska, S., Tanaka, K., Tanaka, N., Tu, K.P., Von Randow, C., 2009. The land-atmosphere water flux in the tropics. *Global Change Biology* 15 (11), 2694–2714.
- Foken, T., Wichura, B., 1996. Tools for quality assessment of surface-based flux measurements. *Agricultural and Forest Meteorology* 78 (1–2), 83–105.
- Gilmanov, T.G., Aires, L., Barcza, Z., Baron, V.S., Beletti, L., Beringer, J., Billesbach, D., Bonal, D., Bradford, J., Ceschia, E., Cook, D., Corradi, C., Frank, A., Gianelle, D., Gimeno, C., Gruenwald, T., Guo, H.Q., Hanan, N., Haszpra, L., Heilman, J., Jacobs, A., Jones, M.B., Johnson, D.A., Kiely, G., Li, S.G., Magliulo, V., Moors, E., Nagy, Z., Nasyrov, M., Owensby, C., Pinter, K., Pio, C., Reichstein, M., Sanz, M.J., Scott, R., Soussana, J.F., Stoy, P.C., Svejcar, T., Tuba, Z., Zhou, G.S., 2010. Productivity respiration, and light-response parameters of world grassland and agroecosystems derived from flux-tower measurements. *Rangeland Ecology & Management* 63 (1), 16–39.
- Goulden, M.L., Miller, S.D., da Rocha, H.R., Menton, M.C., de Freitas, H.C., Figueira, A., de Sousa, C.A.D., 2004. Diel and seasonal patterns of tropical forest CO₂ exchange. *Ecological Applications* 14 (4), 42–54.
- Grace, J., Mahli, Y., Higuchi, N., Meir, P., 2001. Productivity of tropical forests. In: Roy, J., Saugier, B., Mooney, H. (Eds.), *Terrestrial Global Productivity*. Academic Press, San Diego, CA, USA, pp. 401–426.
- Graham, N.E., Georgakakos, K.P., Vargas, C., Echevers, M., 2006. Simulating the value of El Niño forecasts for the Panama Canal. *Advances in Water Resources* 29 (11), 1665–1677.
- Gu, L.H., Falge, E.M., Boden, T., Baldocchi, D.D., Black, T.A., Saleska, S.R., Suni, T., Verma, S.B., Vesala, T., Wofsy, S.C., Xu, L.K., 2005. Objective threshold determination for nighttime eddy flux filtering. *Agricultural and Forest Meteorology* 128 (3–4), 179–197.
- Hutyra, L.R., Munger, J.W., Saleska, S.R., Gottlieb, E., Daube, B.C., Dunn, A.L., Amaral, D.F., de Camargo, P.B., Wofsy, S.C., 2007. Seasonal controls on the exchange of carbon and water in an Amazonian rain forest. *Journal of Geophysical Research-Biogeosciences* 112. (3).
- IPCC, 2007. *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, Cambridge, United Kingdom, p. 1028.
- IRI, 2010. ENSO Quick Look – A Monthly Summary of the Status of El Niño La Niña and the Southern Oscillation. The International Research Institute for Climate and Society (IRI), <http://iri.columbia.edu/climate/ENSO/currentinfo/QuickLook.html>, 15.01.2010.
- Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E.D., 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* 108 (3), 389–411.
- Kanowski, P., 1997. Plantation forestry for the 21st century. Afforestation and plantation forestry. In: XI World Forestry Congress, Antalya, Turkey, pp. 23–34.
- Kljun, N., Calanca, P., Rotachhi, M.W., Schmid, H.P., 2004. A simple parameterisation for flux footprint predictions. *Boundary-Layer Meteorology* 112 (3), 503–523.
- Lachniet, M.S., 2009. Sea surface temperature control on the stable isotopic composition of rainfall in Panama. *Geophysical Research Letters*, 36.
- Loescher, H.W., Oberbauer, S.F., Gholz, H.L., Clark, D.B., 2003. Environmental controls on net ecosystem-level carbon exchange and productivity in a Central American tropical wet forest. *Global Change Biology* 9 (3), 396–412.
- Malhi, Y., Nobre, A.D., Grace, J., Kruijt, B., Pereira, M.G.P., Culf, A., Scott, S., 1998. Carbon dioxide transfer over a Central Amazonian rain forest. *Journal of Geophysical Research-Atmospheres* 103 (D24), 31593–31612.
- Malhi, Y., Meir, P., Brown, S., 2002. Forests, carbon and global climate. *Philosophical Transactions of the Royal Society of London Series A – Mathematical Physical and Engineering Sciences* 360 (1797), 1567–1591.
- Malmer, A., Murdiyarso, D., Bruijnzeel, L.A., Ilstedt, U., 2010. Carbon sequestration in tropical forests and water: a critical look at the basis for commonly used generalizations. *Global Change Biology* 16 (2), 599–604.
- Mauder, M., Foken, T., Clement, R., Elbers, J.A., Eugster, W., Grunwald, T., Heusinkveld, B., Kolle, O., 2008. Quality control of CarboEurope flux data – Part 2: inter-comparison of eddy-covariance software. *Biogeosciences* 5 (2), 451–462.
- Moffat, A.M. A new methodology to interpret high resolution measurements of net carbon fluxes between terrestrial ecosystems and the atmosphere. PhD thesis, Friedrich Schiller University, Jena, unpublished.
- Monteith, J.L., Unsworth, M.H., 1990. *Principles of Environmental Physics*. Edward Arnold, London, p. 291.
- Moureaux, C., Debaq, A., Bodson, B., Heinesch, B., Aubinet, M., 2006. Annual net ecosystem carbon exchange by a sugar beet crop. *Agricultural and Forest Meteorology* 139 (1–2), 25–39.
- Murphy, M., Balsler, T., Buchmann, N., Hahn, V., Potvin, C., 2008. Linking tree biodiversity to belowground process in a young tropical plantation:

- impacts on soil CO₂ flux. *Forest Ecology and Management* 255 (7), 2577–2588.
- NOAA, 2010. National Weather Service, JetStream – Online School for Weather. National Oceanic and Atmospheric Administration (NOAA), http://www.srh.noaa.gov/jetstream//tropics/ensso_impacts.htm, 15.01.2010.
- Phillips, O.L., Aragao, L., Lewis, S.L., Fisher, J.B., Lloyd, J., Lopez-Gonzalez, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., van der Heijden, G., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T.R., Banki, O., Blanc, L., Bonal, D., Brando, P., Chave, J., de Oliveira, A.C.A., Cardozo, N.D., Czimczik, C.I., Feldpausch, T.R., Freitas, M.A., Gloor, E., Higuchi, N., Jimenez, E., Lloyd, G., Meir, P., Mendoza, C., Morel, A., Neill, D.A., Nepstad, D., Patino, S., Penuela, M.C., Prieto, A., Ramirez, F., Schwarz, M., Silva, J., Silveira, M., Thomas, A.S., ter Steege, H., Stropp, J., Vasquez, R., Zelazowski, P., Davila, E.A., Andelman, S., Andrade, A., Chao, K.J., Erwin, T., Di Fiore, A., Honorio, E., Keeling, H., Killeen, T.J., Laurance, W.F., Cruz, A.P., Pitman, N.C.A., Vargas, P.N., Ramirez-Angulo, H., Rudas, A., Salamao, R., Silva, N., Terborgh, J., Torres-Lezama, A., 2009. Drought sensitivity of the Amazon rainforest. *Science* 323 (5919), 1344–1347.
- Priante-Filho, N., Vourlitis, G.L., Hayashi, M.M.S., Nogueira, J.D., Campelo, J.H., Nunes, P.C., Souza, L.S.E., Couto, E.G., Hoeger, W., Raiter, F., Trienweiler, J.L., Miranda, E.J., Priante, P.C., Fritzen, C.L., Lacerda, M., Pereira, L.C., Biudes, M.S., Suli, G.S., Shiraiwa, S., Do Paulo, S.R., Silveira, M., 2004. Comparison of the mass and energy exchange of a pasture and a mature transitional tropical forest of the southern Amazon Basin during a seasonal transition. *Global Change Biology* 10 (5), 863–876.
- Sakai, R.K., Fitzjarrald, D.R., Moraes, O.L.L., Staebler, R.M., Acevedo, O.C., Czikowsky, M.J., Da Silva, R., Brait, E., Miranda, V., 2004. Land-use change effects on local energy, water, and carbon balances in an Amazonian agricultural field. *Global Change Biology* 10 (5), 895–907.
- Saleska, S.R., Miller, S.D., Matross, D.M., Goulden, M.L., Wofsy, S.C., da Rocha, H.R., de Camargo, P.B., Crill, P., Daube, B.C., de Freitas, H.C., Hutryra, L., Keller, M., Kirchhoff, V., Menton, M., Munger, J.W., Pyle, E.H., Rice, A.H., Silva, H., 2003. Carbon in Amazon forests: unexpected seasonal fluxes and disturbance-induced losses. *Science* 302 (5650), 1554–1557.
- Santos, A.J.B., Quesada, C.A., Da Silva, G.T., Maia, J.F., Miranda, H.S., Miranda, A.C., Lloyd, J., 2004. High rates of net ecosystem carbon assimilation by Brachiaria pasture in the Brazilian Cerrado. *Global Change Biology* 10 (5), 877–885.
- Scherer-Lorenzen, M., Bonilla, J.L., Potvin, C., 2007. Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment. *Oikos* 116 (12), 2108–2124.
- Schwalm, C.R., Williams, C.A., Schaefer, K., Arneth, A., Bonal, D., Buchmann, N., Chen, J.Q., Law, B.E., Lindroth, A., Luysaert, S., Reichstein, M., Richardson, A.D., 2010. Assimilation exceeds respiration sensitivity to drought: a FLUXNET synthesis. *Global Change Biology* 16 (2), 657–670.
- STRI, 2010. Physical Monitoring Program. Smithsonian Tropical Research Institute (STRI), http://striweb.si.edu/esp/physical_monitoring/index_phy_mon.htm, 15.01.2010.
- Trenberth, K.E., Fasullo, J.T., 2010. Climate change tracking Earth's energy. *Science* 328 (5976), 316–317.
- Vargas, R., Baldocchi, D.D., Querejeta, J.I., Curtis, P.S., Hasselquist, N.J., Janssens, I.A., Allen, M.F., Montagnani, L., 2010. Ecosystem CO₂ fluxes of arbuscular and ectomycorrhizal dominated vegetation types are differentially influenced by precipitation and temperature. *New Phytologist* 185 (1), 226–236.
- von Randow, C., Manzi, A.O., Kruijt, B., de Oliveira, P.J., Zanchi, F.B., Silva, R.L., Hodnett, M.G., Gash, J.H.C., Elbers, J.A., Waterloo, M.J., Cardoso, F.L., Kabat, P., 2004. Comparative measurements and seasonal variations in energy and carbon exchange over forest and pasture in South West Amazonia. *Theoretical and Applied Climatology* 78 (1–3), 5–26.
- Vourlitis, G.L., Priante, N., Hayashi, M.M.S., Nogueira, J.D., Caseiro, F.T., Campelo, J.H., 2001. Seasonal variations in the net ecosystem CO₂ exchange of a mature Amazonian transitional tropical forest (cerradao). *Functional Ecology* 15 (3), 388–395.
- Wang, W., Fang, J.Y., 2009. Soil respiration and human effects on global grasslands. *Global and Planetary Change* 67 (1–2), 20–28.
- Webb, E.K., Pearman, G.I., Leuning, R., 1980. Correction of flux measurements for density effects due to heat and water-vapor transfer. *Quarterly Journal of the Royal Meteorological Society* 106 (447), 85–100.
- White, R., Murray, S., Rohweder, M., 2000. Pilot Analysis of Global Ecosystems (PAGE), Grassland Ecosystems. World Resources Institute, Washington, DC, p. 81.
- Wilsey, B.J., Parent, G., Roulet, N.T., Moore, T.R., Potvin, C., 2002. Tropical pasture carbon cycling: relationships between C source/sink strength, above-ground biomass and grazing. *Ecology Letters* 5 (3), 367–376.
- Wilson, K., Goldstein, A., Falge, E., Aubinet, M., Baldocchi, D., Bernhofer, P., Bernhofer, C., Ceulemans, R., Dolman, H., Field, C., Grelle, A., Ibrom, A., Law, B.E., Kowalski, A., Meyers, T., Moncrieff, J., Monson, R., Oechel, W., Tenhunen, J., Valentini, R., Verma, S., 2002. Energy balance closure at FLUXNET sites. *Agricultural and Forest Meteorology* 113 (1–4), 223–243.
- Wolf, S., Eugster, W., Potvin, C., Turner, B.L., Buchmann, N. Carbon sequestration potential of tropical pasture compared to afforestation in Panama. *Global Change Biology*, in revision.