

Carbon sequestration potential of tropical pasture compared with afforestation in Panama

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Abstract

Tropical forest ecosystems play an important role in regulating the global climate, yet deforestation and land-use change mean that the tropical carbon sink is increasingly influenced by agroecosystems and pastures. Despite this, it is not yet fully understood how carbon cycling in the tropics responds to land-use change, particularly for pasture and afforestation. Thus, the objectives of our study were: (1) to elucidate the environmental controls and the impact of management on gross primary production (GPP), total ecosystem respiration (TER) and net ecosystem CO₂ exchange (NEE); (2) to estimate the carbon sequestration potential of tropical pasture compared with afforestation; and (3) to compare eddy covariance-derived carbon budgets with biomass and soil inventory data. We performed comparative measurements of NEE in a tropical C₄ pasture and an adjacent afforestation with native tree species in Sardinilla (Panama) from 2007 to 2009. Pronounced seasonal variation in GPP, TER and NEE were closely related to radiation, soil moisture, and C₃ vs. C₄ plant physiology. The shallow rooting depth of grasses compared with trees resulted in a higher sensitivity of the pasture ecosystem to water limitation and seasonal drought. During 2008, substantial amounts of carbon were sequestered by the afforestation (−442 g C m^{−2}, negative values denote ecosystem carbon uptake), which was in agreement with biometric observations (−450 g C m^{−2}). In contrast, the pasture ecosystem was a strong carbon source in 2008 and 2009 (261 g C m^{−2}), associated with seasonal drought and overgrazing. In addition, soil carbon isotope data indicated rapid carbon turnover after conversion from C₄ pasture to C₃ afforestation. Our results clearly show the potential for considerable carbon sequestration of tropical afforestation and highlight the risk of carbon losses from pasture ecosystems in a seasonal tropical climate.

Keywords: carbon dioxide fluxes, eddy covariance, FLUXNET, grazing, land-use change, managed ecosystems, soil carbon

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Introduction

Tropical ecosystems account for more than half of the global terrestrial gross primary production (GPP) (Beer *et al.*, 2010), contain 40% of the carbon stored in the terrestrial biosphere, and are considered to sequester large amounts of carbon dioxide from the atmosphere (Grace *et al.*, 2001). However, the current role of tropical ecosystems in terrestrial carbon sequestration remains uncertain as ongoing deforestation and associated land-use changes strongly reduce the area of tropical forests, with cropland and pasture becoming more prevalent (Fearnside 2005; Alves *et al.*, 2009). Land-use change from tropical forest to pasture has been reported to affect ecosystem carbon budgets in the short-term through increased inter and intra-annual variations in ecosystem

CO₂ fluxes and the sensitivity to seasonal drought (Priante-Filho *et al.*, 2004; von Randow *et al.*, 2004; Saleska *et al.*, 2009). Moreover, one of the major long-term effects of such land-use changes is the reduced carbon sink strength of pasture ecosystems (IPCC 2007).

Despite the general importance of tropical ecosystems for global climate and carbon cycling, eddy covariance (EC) flux measurements in the tropics remain scarce and thus are globally under-represented. Tropical sites represent only 10% of the global FLUXNET measurement network, with most sites located in neotropical forests and only a few in tropical pastures or other land-use types (<http://www.fluxnet.ornl.gov>). A recent FLUXNET synthesis highlighted the importance of C₄ vegetation for terrestrial GPP, accounting for 20% of global terrestrial GPP, and emphasized the need for an expansion of observations in these scarcely covered ecosystems (Beer *et al.*, 2010).

EC flux measurements indicate that many tropical forests act as carbon sinks, which is consistent with

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carbon uptake inferred from long-term biometric data at some of these sites (Malhi *et al.*, 1999; Loescher *et al.*, 2003; Luysaert *et al.*, 2007; Bonal *et al.*, 2008). A few tropical forests were reported to act as carbon sources, although this might have been related to severe drought or disturbance recovery (Saleska *et al.*, 2003; Hutyra *et al.*, 2007). In Brazil, a transitional forest was found to have an annual carbon budget close to equilibrium (Vourlitis *et al.*, 2001) while a tropical savanna appeared to be a sink of carbon (Miranda *et al.*, 1997). Published results of carbon fluxes for other land-use types in the neotropics are limited: again in Brazil, Grace *et al.* (1998) and von Randow *et al.* (2004) found indications that a tropical pasture sequestered carbon, as did Priante-Filho *et al.* (2004) for a pasture under conversion to afforestation. In contrast, chamber measurements by Wilsey *et al.* (2002) showed carbon losses from tropical pastures in Panama. It therefore remains unclear whether tropical pastures are carbon sinks or sources.

Latin America has one of the highest deforestation rates in the tropics, with land predominantly converted to pasture for extensive grazing (Wassenaar *et al.*, 2007). Few of these pastures are later used for afforestation, although this is considered an effective measure to sequester carbon and mitigate increasing CO₂ concentrations in the atmosphere (FAO 2009). Malhi *et al.* (2002) estimated the mitigation potential of tropical afforestation at 15% of global CO₂ emissions. Afforestation of pasture may become more relevant for tropical countries in the future within the international carbon accounting of the Kyoto protocol, but this requires accurate information on the carbon sequestration potential involved.

A comparative measurement design is needed to quantify carbon dynamics involved in the land-use change from pasture to afforestation, to account for confounding factors of spatial divergence and variations in meteorology (Don *et al.*, 2009). In this study, we determined the carbon budgets of tropical pasture and native tree species afforestation at a site in Central Panama from 2007 to 2009 based on continuous measurements using two EC flux towers. The objectives of our study were: (1) to elucidate the environmental controls and the impact of management on GPP, total ecosystem respiration (TER) and net ecosystem CO₂ exchange (NEE); (2) to estimate the carbon sequestration potential of tropical pasture compared with afforestation; and (3) to compare EC-derived carbon budgets with biomass and soil inventory data.

Material and methods

Site description

The Sardinilla site (Panama) is located at 9°19' N, 79°38' W and 70 m a.s.l., about 30 km north-east of Barro Colorado Island

(BCI). Sardinilla has a semi-humid tropical climate with a mean annual temperature of 25.2 °C, 2289 mm annual precipitation (2007–2009; long-term mean of nearby Salamanca 1972–2009 is 2267 mm) and a pronounced dry season from January to April. Dry season length in Central Panama varies among years (134 ± 19 days for 1954–2009; ACP, 2010) and is – along with precipitation patterns – influenced by ENSO, the El Niño Southern Oscillation (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 in the pasture are Alfisols, based on their high base status and clay translocation in the profile. Soils in the afforestation are similar and include as well large areas with cracking clays that exhibit vertic properties. The Sardinilla site was logged in 1952/1953 and shortly used as arable land, before it was converted to pasture (Wilsey *et al.*, 2002). An improved afforestation (i.e., plantation using native tree species only) was established at parts of the site (7.5 ha) in 2001 with an average of 1141 stems per ha and without any particular soil preparation (ploughing). The six native tree species used for the afforestation site were: *Luehea seemanii*, *Cordia alliodora*, *Anacardium excelsum*, *Hura crepitans*, *Cedrela odorata*, *Tabebuia rosea*. A moderately dense understory vegetation (shrubs, grasses and sedges) was present, which was cut once a year (typically in December) by manual thinning and the residues left on-site. Traditional grazing continued on an adjacent pasture (6.5 ha), where vegetation is dominated by C₄ grasses, and consists of (most abundant first): *Paspalum dilatatum* (C₄), *Rhynchospora nervosa* (sedge, C₃), *Panicum dichotomiflorum* (C₄) and *Sporobolus indicus* (C₄). Mean canopy height was about 10 m in the afforestation and 0.09 m in the pasture (in 2008). While the afforestation site has an undulating topography (elevation range <10 m), the adjacent pasture is homogeneously flat with an overall slope of <2°. Detailed footprint analyses indicated that fluxes measured at both sites indeed originate predominantly from the respective land-use type (Wolf *et al.*, 2011). For further details on the Sardinilla sites see Wolf *et al.* (2011).

Instrumentation and data acquisition

Two flux towers were established in Sardinilla over a grazed pasture (March 2007–January 2010), and an adjacent afforestation (February 2007–June 2009). Our micrometeorological measurement systems consisted of an open path infrared gas analyzer (IRGA, Li-7500, LI-COR, Lincoln, NE, USA) and a three-dimensional sonic anemometer (CSAT3, Campbell Scientific, Logan, IL, USA). Instruments were installed at a height of 3 m at the pasture and 15 m at the afforestation site. Data acquisition was performed using 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). Ancillary meteorological measurements included air temperature and relative humidity (MP100A, Rotronic, Bassersdorf, Switzerland), incoming shortwave radiation (R_G , CM3, Kipp & Zonen, Delft, The Netherlands), photosynthetic photon flux density (PPFD,

PAR Lite, Kipp & Zonen), precipitation (10116 rain gauge, TOSS, Potsdam, Germany), 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, WA, 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). Precipitation and incoming shortwave radiation were measured at one tower location only. Regular cleaning of sensors and IRGA calibration checks were carried out to assure data quality. Further details on the measurement setup at the Sardinilla site are reported in Wolf *et al.* (2011).

Flux data processing

Data acquisition and quality filtering. Flux measurements were recorded using the in-house software sonicreadHS and raw data were processed to half-hourly averages using the in-house EC software eth-flux (Mauder *et al.*, 2008; source code for Unix/Linux systems can be obtained from the authors). During post-processing, fluxes were corrected for damping losses (Eugster & Senn, 1995) and density fluctuations (Webb *et al.*, 1980). Data screening was done using the following rejection criteria: (1) Optical sensor contamination (spider eggs, rain) resulting in high window dirtiness of the IRGAs. We used a 10% threshold above the mean background value of the respective IRGA. (2) Filtering for stationarity following Foken & 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^*). Seasonal and site-dependent u^* -thresholds were determined according to the method by Gu *et al.* (2005) and Moureaux *et al.* (2006). These thresholds yielded $u^* < 0.04 \text{ m s}^{-1}$ during the dry season, $u^* < 0.03 \text{ m s}^{-1}$ during the dry-wet transition, while no thresholds were found during the wet season and wet-dry transition periods for the pasture site. At the afforestation site, the thresholds determined were $u^* < 0.02 \text{ m s}^{-1}$ during the dry season, $u^* < 0.01 \text{ m s}^{-1}$ during the wet season, $u^* < 0.05 \text{ m s}^{-1}$ during the dry-wet transition, while no threshold was found during the wet-dry transition period. (6) Negative nighttime fluxes and a respective amount of positive nighttime data were removed using a trimmed mean approach.

Gap filling

Filling of data gaps was required to obtain a continuous time series of flux data for budget assessments. At the pasture site, data were available for 97.7% of the time between June 2007 and January 2010. After quality filtering, 54.6% of good to excellent quality data remained (64.7% daytime, 43.6% nighttime data). At the afforestation site, data availability was 94.5% between June 2007 and June 2009, with 47.6% of good to

excellent quality data remaining after quality filtering (65.4% daytime, 28.3% nighttime data).

Gap filling of NEE_{daytime} was based on non-linear light response curves (LRC), i.e., the functional relationship between daytime CO₂ fluxes and photosynthetic photon flux density (PPFD). We used a logistic sigmoid function as suggested by Moffat (unpublished) that has been used by Eugster *et al.* (2010) to determine light-response parameters for each single day:

$$NEE_{\text{daytime}} = 2A_{\text{max}} \left(0.5 - \frac{1}{1 + e^{-\frac{2\alpha \text{PPFD}}{A_{\text{max}}}}} \right) + TER_{\text{daytime}} \quad (1)$$

A_{max} denotes the maximum photosynthetic capacity of the ecosystem ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), α the apparent quantum yield ($\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photons), PPFD the photosynthetic photon flux density ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, 90% quantile used to exclude outliers) and TER_{daytime} the daytime TER ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). The initial value of α was set to 0.03 and the initial value of TER_{daytime} was determined using a linear least-squares regression. The applied sigmoid fit overcomes some of the limitations of the widely used rectangular (Michaelis–Menten equation) and nonrectangular hyperbolic fits (Gilmanov *et al.*, 2003). In particular, it was found to yield the best light response approximation of all semiempirical functions by properly describing the different phases of the light response of NEE_{daytime} (Eugster *et al.*, 2010; Moffat unpublished). For days, when the logistic sigmoid function did not converge or the curvature in the relationship between NEE_{daytime} and PPFD was not significant, a linear least-squares regression was used. Remaining daytime gaps (e.g. due to few or no measurements) were filled using a gap model with parameters estimated from the LRC of the days prior and subsequent to the gaps, or using linear interpolation. During nighttime, we found only a weak temperature sensitivity of ecosystem respiration to soil and air temperatures ($R^2 < 0.02$), irrespective of the choice of nonlinear (Lloyd and Taylor model, Q_{10}) or linear functions. Therefore, we gap filled nighttime data using a 10-day running mean approach. Few nighttime gaps that still remained (<1%) at the afforestation site were filled using linear interpolation.

Partitioning

To partition the comparably small flux of daytime NEE into its much larger gross components, we used:

$$GPP = -NEE_{\text{daytime}} + TER \quad (2)$$

with GPP (positive value) inferred from the difference of daytime net ecosystem exchange (NEE_{daytime}) and TER . TER was inferred from mean nighttime data (as no temperature sensitivity was observed, cf. Gap Filling section), when photosynthesis is zero (and thus GPP is zero). In cases when NEE_{daytime} exceeded TER (resulting in negative GPP values), e.g. with onset of turbulent mixing in the morning or after rainfall, we replaced TER derived from nighttime data with NEE_{daytime} and set GPP to zero. Since our daytime TER is inferred from mean nighttime data without a temperature dependency observed in Sardinilla, no diurnal variations in TER are

assumed. In general, daytime TER inferred from nighttime data should be considered as best estimate, since it neglects photorespiration occurring during the day. While this is a valid assumption for our pasture site which is dominated by C₄ vegetation, this assumption is more critical for our afforestation site which is dominated by C₃ vegetation, although TER during the day is typically dominated by soil respiration.

LAI, biomass, grazing and soil measurements

Auxiliary variables included leaf area index (LAI) and standing biomass measurements, stocking densities and soil sampling. Leaf area index (LAI) was measured in campaigns with a LAI-2000 (LI-COR, Lincoln, USA) in July 2008 and weekly till bi-weekly from March to July 2009. At the afforestation site, 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). In the pasture, aboveground standing biomass was sampled bi-weekly ($n = 10$) from June 2008 to January 2010 using a 50 × 50 cm aluminium frame with subsequent drying for at least 3 days at 60 °C. Since February 2009, photosynthetic active (green) biomass was separated from senescent biomass. Based on the measurements from 2009 and 2010, we estimated the percentage of living biomass before March 2009. Total aboveground biomass carbon at the pasture was calculated by assuming that 50% of the dry weight green biomass is carbon.

Grazing (i.e., stocking density) at the pasture was monitored between June 2008 and January 2010 by counting the number of grazing livestock (dominantly cattle with a few horses) on a daily basis. We used coefficients reported by Chilonda & Otte (2006) to calculate standardized livestock units (LU) per hectare, with cattle accounting for 0.7 LU and horses for 0.5 LU in Central America. Overgrazing was defined as $> 4 \text{ LU ha}^{-1} \text{ d}^{-1}$, which is rather conservative with respect to generally accepted values of the carrying capacity of 1–2 LU ha⁻¹ in Europe.

At the afforestation site, standing biomass was assessed using annually measured biometric data for trees (calculated based on allometric equations; on 22 plots of 45 × 45 m size), herbaceous plants, litter and coarse woody debris (CWD). Details on the assessment of biometric data can be found in Potvin *et al.* (2011). As herbaceous biomass data were not available for 2009, we assumed no change from 2008. Data on CWD were not available for the years 2007 and 2009, and thus, we estimated CWD by averaging the data from available years.

Since the year 2008 was the only calendar year with full data coverage by EC measurements at the afforestation, our direct comparison with inventory data was initially constrained to that specific year. However, we used our EC measurements from 2008 to estimate fluxes from January to May of the year 2007, and July to December 2009. This extrapolation made it possible to compare 3 years of EC fluxes with the biomass inventory at the afforestation.

Topsoil (0–10 cm) sampling at the afforestation was done in March 2009 ($n = 22$) using a cylindrical corer 10 cm long with a diameter of 6.8 cm. At the pasture site, three soil profiles from 0 to 100 cm depth were sampled horizontally in January 2010, in

10 cm increments, and additional samples in 5 cm depth. Topsoil values at the pasture were derived by averaging the samples from 5 and 10 cm depth. All samples were dried at 60 °C for at least 72 h before they were ground and analyzed for C, N and $\delta^{13}\text{C}$ with an elemental analyzer (Thermo Flash HT Soil Analyzer, Thermo Fisher Scientific, Waltham, USA) coupled through a ConFlo III interface to an isotope ratio mass spectrometer (Delta V Advantage, Thermo Fisher Scientific, Waltham, USA). To assess changes in soil parameters since afforestation establishment, we compared our measurements with samplings from June 2001 and 2002 by Abraham (2004). We used bulk density (d_B) values reported by Abraham (2004) to calculate topsoil (0–10 cm) carbon and nitrogen pools, by assuming no changes in d_B since 2001/2002. This is supported by a study of Seitlinger (2008) that found no changes of topsoil d_B in the afforestation between 2001 and June 2007. Data on carbon pools below 10 cm at the afforestation site was extracted from Abraham (2004), assuming changes in carbon pools since 2001 occurred predominantly in the topsoil, as deeper soil carbon pools are considered relatively stable (Malhi & Davidson, 2009). At the pasture site, we used the mean of the three soil profiles sampled in 2010 and the topsoil d_B reported by Abraham (2004) to estimate soil carbon pools from 0–100 cm. A mixing model was used to assess the carbon isotopic source contribution of organic matter in the soil, with litter values reported by Abraham (2004) as -14.4‰ for pasture and -29.5‰ for tree litter.

Statistical analyses and general conventions

All statistical analyses were carried out using the R statistics software package, version 2.10.0 (R Development Core Team 2009, www.r-project.org). Daytime was defined as the period when PPFD exceeded $5 \mu\text{mol m}^{-2} \text{ s}^{-1}$. Fluxes from the atmosphere to the biosphere are marked with a negative sign denoting carbon uptake by the ecosystem; positive fluxes indicate carbon loss. In general, only seasons with full data coverage were used for seasonal averaging. Separation of dry from wet seasons and transition periods was done based on daily precipitation sums using the methodology described in Wolf *et al.* (2011): wet season was defined as the time span with no periods of more than four consecutive days without rain, and the dry season *vice versa*. Transition periods mark the time span between both main seasons. When writing 'seasonal drought', we refer to the plant physiological effects of soil moisture deficiency during the dry season.

Results

Intra- and interannual variations in precipitation

We found a pronounced seasonality in the climate in Sardinilla where most of the precipitation ($> 98\%$) occurred during the wet season from April to December (Table 1, Fig. 1d). On average, November was the wettest ($> 300 \text{ mm}$) and September was the driest month (about 200 mm) during the wet season. The dry season lasted

Table 1 Monthly values of, precipitation sum (P), mean soil water content (SWC, Sardinilla afforestation, at 5 cm depth), total photosynthetic photon flux density (PPFD), mean air temperature (T_{Air}), total net ecosystem exchange (NEE), total gross primary production (GPP) and total ecosystem respiration (TER) at Sardinilla, Panama from 2007 to 2009. Measurements at the afforestation were discontinued after June 2009

Year	Month	P (mm)	SWC (%)	PPFD (mol m^{-2})	T_{Air} ($^{\circ}\text{C}$)	Pasture			Afforestation			
						NEE (g C m^{-2})	GPP (g C m^{-2})	TER (g C m^{-2})	NEE (g C m^{-2})	GPP (g C m^{-2})	TER (g C m^{-2})	
2007	Jun	278	40.5	802	25.5	9.3	216	225	-41.4	211	170	
	Jul	197	43.7	815	25.3	3.8	225	229	-26.7	200	174	
	Aug	223	45.9	814	25.0	6.9	215	222	-23.4	188	164	
	Sep	206	48.2	901	25.1	-13.5	239	226	-36.2	196	160	
	Oct	380	47.2	867	25.1	-13.8	240	226	-39.9	201	161	
	Nov	351	51.6	751	24.9	-19.5	219	199	-31.1	184	153	
	Dec	288	49.8	942	24.7	-23.9	253	229	-1.5	150	148	
	2008	Jan	11	28.3	1290	24.6	16.6	270	287	-27.6	168	140
		Feb	11	24.0	1152	24.6	54.5	144	199	-42.2	155	112
		Mar	4	22.3	1350	24.9	69.0	72	141	-27.0	135	108
		Apr	72	22.1	1249	25.5	98.4	68	166	8.7	119	127
		May	289	30.7	985	25.5	62.8	173	236	-3.4	183	180
Jun		230	42.8	781	25.1	8.6	210	219	-43.7	199	155	
Jul		356	49.9	825	24.6	-19.5	239	220	-58.1	206	148	
Aug		263	50.3	874	24.9	-9.8	225	215	-59.4	207	148	
Sep		203	49.5	934	25.5	-7.9	225	218	-44.7	189	145	
Oct		241	49.1	945	25.2	-16.0	260	245	-61.2	199	138	
Nov		338	51.9	680	24.3	-9.2	202	193	-57.2	169	112	
Dec		53	45.9	1149	25.1	13.4	257	270	-26.0	154	128	
2009	Jan	13	30.2	1125	24.7	31.7	211	242	-30.7	153	122	
	Feb	20	29.1	1121	25.3	71.6	94	166	-40.7	133	93	
	Mar	12	25.8	1373	25.2	75.9	51	127	-11.2	114	103	
	Apr	94	23.9	1235	25.8	87.2	25	112	22.1	86	108	
	May	239	32.0	958	25.7	73.4	145	219	13.3	148	162	
	Jun	238	39.1	953	25.5	33.2	177	210	-60.8	212	151	
	Jul	309	-	982	26.1	-3.3	226	223	-	-	-	
	Aug	286	-	923	25.7	-22.1	233	210	-	-	-	
	Sep	211	-	913	26.0	-36.5	231	194	-	-	-	
	Oct	296	-	894	25.3	-40.7	251	211	-	-	-	
	Nov	486	-	595	24.7	-10.5	202	192	-	-	-	
	Dec	30	-	1112	25.5	-0.2	246	245	-	-	-	

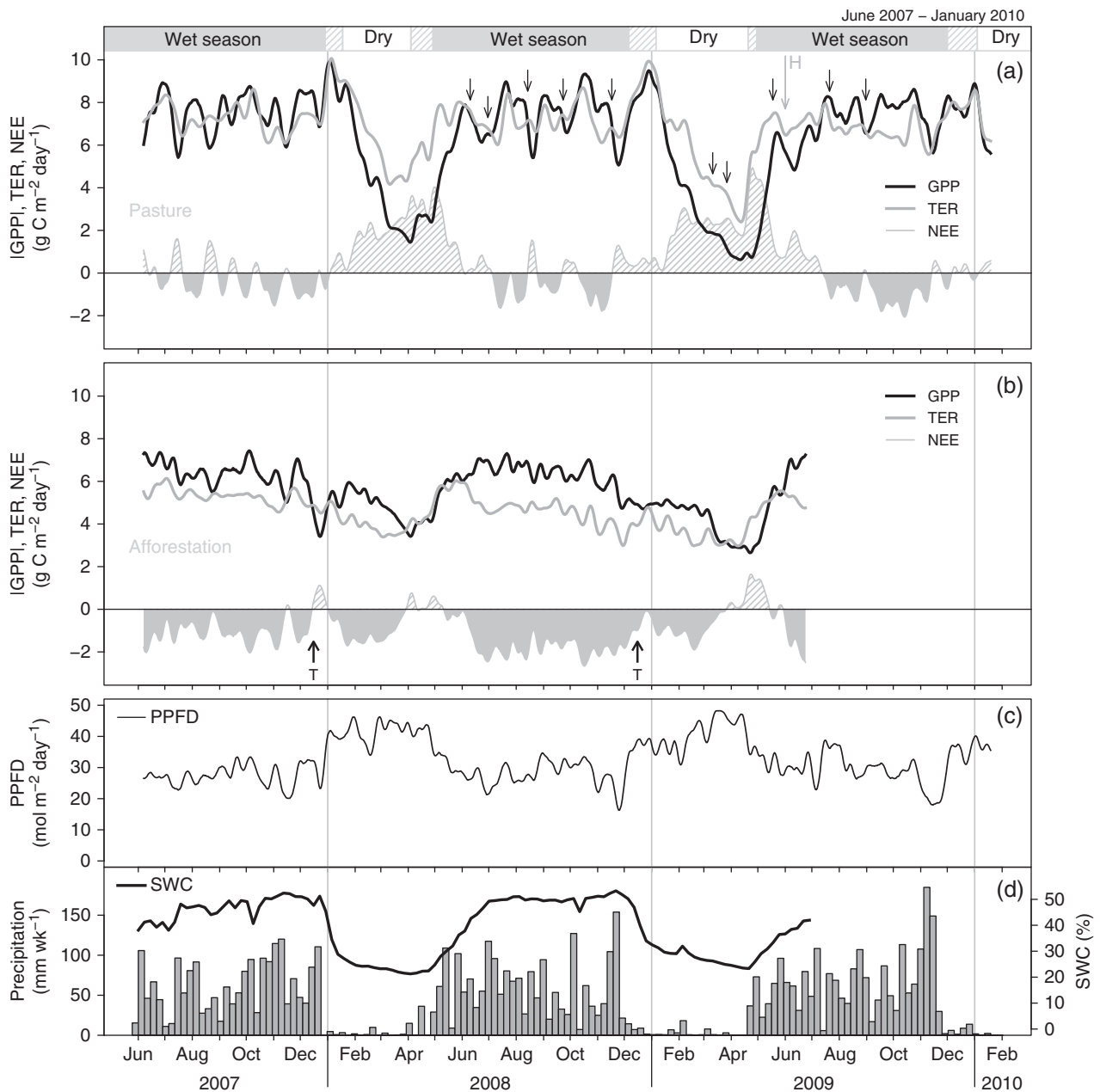


Fig. 1 Daily total gross primary production ($IGPP$, absolute value), total ecosystem respiration (TER) and net ecosystem exchange (NEE ; full shading indicates periods of carbon sinks, striped periods of carbon sources) of the Sardinilla pasture (a) and afforestation (b) sites. Daily total of photosynthetic photon flux density ($PPFD$) is shown from June 2007 to January 2010 (c). $IGPP$, TER , NEE and $PPFD$ are displayed as 14-days running means. Black arrows denote first day of periods with overgrazing ($> 4 \text{ LU ha}^{-1} \text{ day}^{-1}$) and 'H' combined with grey arrow marks the day of herbicide application by the farmer at the pasture. 'T' combined with the black arrow indicates periods of understory thinning at the afforestation. Weekly precipitation (grey bars) and weekly mean volumetric soil water content (SWC ; Sardinilla afforestation, at 5 cm depth) are given (d). Measurements at the afforestation were discontinued after June 2009. The inserts at the top indicate the different seasons (wet, dry) including transition periods (shaded areas).

from about January to April. The two transition periods were characterized by highly variable but limited amounts of precipitation ($< 4 \text{ mm d}^{-1}$). Compared with the long-term annual mean from nearby Salamanca

(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%).

Soil water content (SWC) at 5 cm depth exceeded 40% during most of the wet season (mean 46%, maximum of 52% in November) and rapidly declined to below 30% after the onset of the dry season (mean 26%, minimum of 22% in April; Table 1, Fig. 1d). Following the first rainfalls during the dry-wet transition period in April, SWC started to increase swiftly and exceeded 40% by June. During the dry season in 2009, SWC declined less compared with 2008, which was related to moderate precipitation events in February. SWC in deeper soil layers (30 cm, not shown) was higher compared with SWC in 5 cm depth during the dry season and about similar during the wet season. Daily total photosynthetic photon flux density (PPFD) ranged from a minimum of $5.2 \text{ mol m}^{-2} \text{ d}^{-1}$ in November (wet season) to a maximum of $58.5 \text{ mol m}^{-2} \text{ d}^{-1}$ in March (dry season; Fig. 1c). PPFD exceeded $40 \text{ mol m}^{-2} \text{ d}^{-1}$ during most of the dry season (mean $41.8 \text{ mol m}^{-2} \text{ d}^{-1}$) and was reduced during the wet season (mean $28.6 \text{ mol m}^{-2} \text{ d}^{-1}$). Seasonal temperature variations at Sardinilla were small and within $\pm 1^\circ \text{C}$ of the annual mean of 25.2°C (2007–2009), with the lowest values generally occurring during November to March (Table 1). The diurnal temperature range in Sardinilla was larger than seasonal variations and ranged from 22.2°C (nighttime) to 27.4°C (daytime) during the dry season and 23.5°C to 26.8°C during the wet season, respectively.

Seasonal patterns in GPP, TER and NEE

We observed strong seasonal variations of GPP, TER and net ecosystem exchange (NEE) in both pasture and afforestation ecosystems. Seasonal variations at both sites were larger during the year 2009 than in 2008 (Fig. 1).

At the pasture site, daily NEE ranged from a minimum of $-4.6 \text{ g C m}^{-2} \text{ d}^{-1}$ during the wet season to a maximum of $8.3 \text{ g C m}^{-2} \text{ d}^{-1}$ during the dry-wet transition period (mean of $0.5 \text{ g C m}^{-2} \text{ d}^{-1}$). During the wet season, average GPP and TER were on the same order of magnitude with seasonal means of $7.0 \text{ g C m}^{-2} \text{ d}^{-1}$. GPP dropped several times by up to 30% during the wet seasons 2007 and 2008 (Fig. 1). We observed maximum values for GPP and TER during the wet-dry transition period, with 8.5 and $8.7 \text{ g C m}^{-2} \text{ d}^{-1}$ respectively (seasonal means). During the dry season, GPP was limited by water availability and declined to a minimum of $2.0 \text{ g C m}^{-2} \text{ d}^{-1}$ (seasonal mean) during the dry-wet transition period with predominantly senescent pasture vegetation (LAI = 0.6). TER was reduced during the dry season as well (mean $5.6 \text{ g C m}^{-2} \text{ d}^{-1}$) but exceeded GPP (mean $3.7 \text{ g C m}^{-2} \text{ d}^{-1}$), resulting in positive NEE and thus, carbon release from the ecosystem. With the first rainfalls during the dry-wet transition period, TER increased rapidly and reached the level of the mean

seasonal TER within about 1 month (Fig. 1). However, with most of the pasture grasses senescent, GPP did not increase for another 1–2 weeks. Maximum carbon losses occurred during the dry-wet transition period. Overall, mean daily TER ($6.89 \pm 1.38 \text{ g C m}^{-2} \text{ d}^{-1}$) was similar to GPP ($6.39 \pm 2.59 \text{ g C m}^{-2} \text{ d}^{-1}$).

At the afforestation site, we observed smaller seasonal variations of NEE, GPP and TER than at the pasture site with lower absolute values in general. Daily NEE ranged from $-5.4 \text{ g C m}^{-2} \text{ d}^{-1}$ during the wet season to $3.7 \text{ g C m}^{-2} \text{ d}^{-1}$ during the dry-wet transition period (mean of $1.0 \text{ g C m}^{-2} \text{ d}^{-1}$). During the wet season, GPP consistently exceeded TER with 6.3 vs. $4.7 \text{ g C m}^{-2} \text{ d}^{-1}$, except during December 2007 (Fig. 1). Accordingly, NEE was negative and the afforestation acted as a carbon sink throughout the wet season. GPP and TER peaked during the early wet season in June and July, after the leaves of all tree species had fully developed (LAI of 6.0 in 2009). Besides a second wet season maximum of GPP during October, GPP and TER declined gradually during the wet season. During the wet-dry transition, TER increased while GPP remained stable. This increase was particularly strong in December 2008 and reduced NEE to $-0.6 \text{ g C m}^{-2} \text{ d}^{-1}$ (seasonal mean). During the dry season, GPP initially increased (in 2007) or remained relatively constant (in 2009) during the early dry season, while TER was declining. However, as GPP exceeded TER, the afforestation maintained carbon uptake during most of the dry season, with a mean NEE of $-0.9 \text{ g C m}^{-2} \text{ d}^{-1}$. During the dry-wet transition, TER increased strongly following the first rainfall while GPP did not increase for another 1–2 weeks. During the dry-wet transition period the afforestation was a carbon source (mean NEE of $0.6 \text{ g C m}^{-2} \text{ d}^{-1}$).

Overall, we observed a strong coupling of daily TER with GPP during the dry season. This coupling was stronger at the pasture ($R^2 = 0.85$, $P < 0.001$) compared with the afforestation ($R^2 = 0.26$, $P < 0.001$). During the wet season, however, daily variations in TER were only weakly correlated with GPP at both sites

Carbon budgets

The pasture ecosystem was a substantial carbon source and lost 470 g C m^{-2} from June 2007 to December 2009. Inter-annual variation in the carbon budget was small, with $261 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 2008 and $260 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 2009 (Fig. 2). Using the mean NEE from January to May 2008 and 2009, we estimated an annual carbon budget of $251 \text{ g C m}^{-2} \text{ yr}^{-1}$ for 2007. The pasture ecosystem lost carbon during most of the year except during the late wet season. Seasonal carbon budgets indicated that more carbon was lost during the dry season 2009 compared with 2008 but losses were in reverse order during the wet

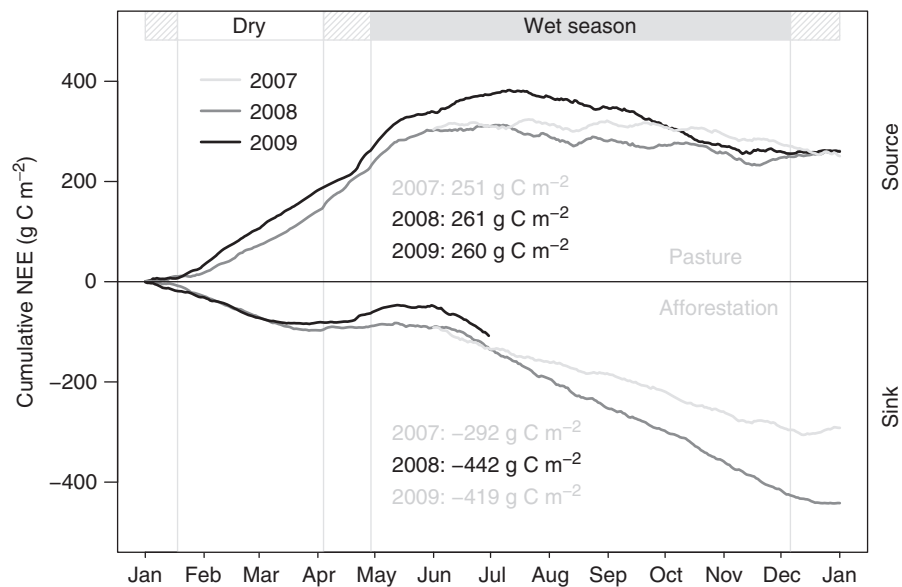


Fig. 2 Cumulative annual net ecosystem exchange (NEE) of the Sardinilla pasture and afforestation sites from 2007 until 2009. Numbers displayed denote annual total budgets with grey indicating years only partly measured. Annual budgets for those years have been estimated using the respective periods from prior and following and years. Annual budget uncertainties are estimated to be below $\pm 100 \text{ g C m}^{-2} \text{ yr}^{-1}$.

Table 2 Season length (d), precipitation sum (P), mean of total daily photosynthetic photon flux density (PPFD) and seasonal total net ecosystem exchange at the pasture (NEE.Pa) and afforestation site (NEE.Aff)

	Dates	Length (d)	P (mm)	PPFD ($\text{mol m}^{-2} \text{ d}^{-1}$)	NEE.Pa (g C m^{-2})	NEE.Aff (g C m^{-2})
2007						
Wet season	23.04.–28.12.	250	2471	27.3*	-43.3*	-198.8*
Wet-dry transition	29.12.–17.01.	20	17	40.8	3.5	-8.2
2008						
Dry season	18.01.–03.04.	77	17	42.1	135.3	-89.6
Dry-wet transition	04.04.–28.04.	25	51	41.8	81.3	7.3
Wet season	29.04.–05.12.	221	1964	28.2	22.0	-337.2
Wet-dry transition	06.12.–05.01.	31	34	37.2	17.6	-18.4
2009						
Dry season	06.01.–19.04.	104	42	41.6	208.9	-75.4
Dry-wet transition	20.04.–29.04.	10	37	34.8	46.5	15.2
Wet season	30.04.–30.11.	215	2122	29.0	-1.7	-44.8*
Wet-dry transition	01.12.–03.01.	34	32	36.6	-1.4	-

*Incomplete, only partial temporal coverage

season 2008 compared with 2009 (Table 2). Total monthly NEE ranged from $-2.3 \text{ g C m}^{-2} \text{ mo}^{-1}$ during the wet season to $92.8 \text{ g C m}^{-2} \text{ mo}^{-1}$ during the dry-wet transition period (overall mean $15.2 \text{ g C m}^{-2} \text{ mo}^{-1}$, Table 1).

The afforestation ecosystem was a strong carbon sink from June 2007 to June 2009 (-750 g C m^{-2}). Total annual NEE was -442 g C m^{-2} in 2008 and we estimated the annual budgets (see pasture) for 2007 and 2009 to -292 and -419 g C m^{-2} , respectively (Fig. 2). The afforestation was a continuous carbon sink during most of

the year, except the end of the dry season, the dry-wet transition period and in December 2007. Seasonal budgets indicated higher carbon losses during the dry-wet transition and onset of the wet season in 2009 compared with 2008 (Table 2). Carbon uptake increased from 2007 to 2009 due to reductions in TER, primarily during the wet season. Monthly NEE ranged from $-36.0 \text{ g C m}^{-2} \text{ mo}^{-1}$ during the wet season to $15.4 \text{ g C m}^{-2} \text{ mo}^{-1}$ during the dry-wet transition period (overall mean $-30.0 \text{ g C m}^{-2} \text{ mo}^{-1}$, Table 1).

During the entire dry season and the beginning of the wet season, the pasture was a persistent and strong source of CO₂. In contrast, the afforestation was a net carbon sink that was only occasionally interrupted during this period (Fig. 1).

Environmental controls of GPP, TER and NEE

SWC and VPD. A strong correlation between monthly mean SWC at 5 cm depth and monthly total NEE was found at the pasture site ($R^2 = 0.84$, $P < 0.001$; not shown). Below a threshold of about 47% in monthly mean SWC at 5 cm depth, the pasture ecosystem became a source of carbon. The ecosystem response of NEE to SWC at 30 cm depth was weaker ($R^2 = 0.64$, $P < 0.001$) compared with 5 cm depth at the pasture site. SWC at 5 cm depth explained less variation in monthly total GPP ($R^2 = 0.59$, $P < 0.001$) and TER ($R^2 = 0.20$, $P < 0.05$) compared with NEE. In addition, we found vapour pressure deficit (VPD) weakly related to NEE ($R^2 = 0.24$, $P < 0.01$) and GPP ($R^2 = 0.23$, $P < 0.01$). Similar but weaker relationships were found on weekly but not on shorter timescales (daily and half-hourly).

At the afforestation site, monthly mean SWC at 30 cm depth showed a stronger relationship to monthly total NEE ($R^2 = 0.39$, $P < 0.01$) compared with SWC at 5 cm depth ($R^2 = 0.26$, $P < 0.01$). GPP was associated even stronger with monthly variations in SWC at 30 cm depth ($R^2 = 0.57$, $P < 0.001$). TER was weakly related to SWC at 5 cm depth only ($R^2 = 0.21$, $P < 0.05$). Unlike at the pasture site, no significant relationship of VPD with NEE was observed, but with GPP ($R^2 = 0.48$, $P < 0.001$) and TER ($R^2 = 0.49$, $P < 0.001$).

PPFD, Ecosystem light response of NEE. We observed a strong seasonality in ecosystem light response to photosynthetic photon flux density (PPFD) with differences between the two sites (Fig. 3). The pasture ecosystem showed a relatively weak light response during the dry season with a high light compensation point (LCP) of $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ and light saturation (due to limited carboxylation rate) at about $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$. This was even more pronounced during the dry-wet transition, light compensation was actually never achieved and TER constantly exceeded photosynthesis. During the wet season, the photosynthetic efficiency was most pronounced with a

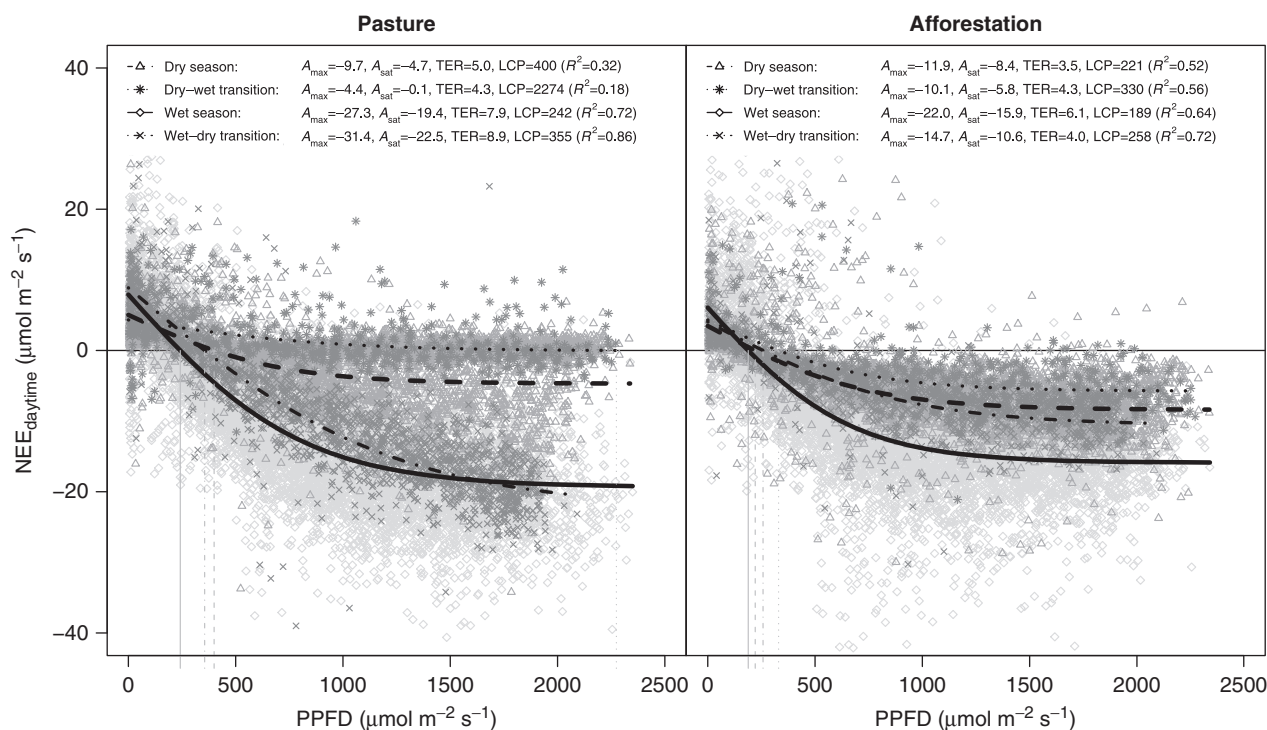


Fig. 3 Seasonally averaged light response curves (LRC) for Sardinilla pasture and afforestation sites from 2007 to 2009. Daytime net ecosystem exchange (NEE_{daytime}) is displayed as a function of photosynthetic photon flux density (PPFD). Symbols denote half-hourly measurements. LRC were estimated using a nonlinear logistic sigmoid function with seasonal fitting parameters: maximum photosynthetic capacity (A_{\max}), saturated photosynthetic capacity (A_{sat}), daytime total ecosystem respiration (TER) and light compensation point (LCP, all in $\mu\text{mol m}^{-2} \text{s}^{-1}$). In addition, seasonal LCPs are represented by the dotted grey lines.

low LCP of $242 \mu\text{mol m}^{-2} \text{s}^{-1}$ and high values of A_{sat} ($-19.4 \mu\text{mol m}^{-2} \text{s}^{-1}$) and $\text{TER}_{\text{daytime}}$ ($7.9 \mu\text{mol m}^{-2} \text{s}^{-1}$). Basically light saturation was not reached during the wet-dry transition period, which exhibited the highest rates of A_{max} ($-31.4 \mu\text{mol m}^{-2} \text{s}^{-1}$) and A_{sat} ($-22.5 \mu\text{mol m}^{-2} \text{s}^{-1}$) along with $\text{TER}_{\text{daytime}}$ ($8.9 \mu\text{mol m}^{-2} \text{s}^{-1}$).

The afforestation ecosystem exhibited less seasonal variation in light response and we observed overall lower LCPs compared with the pasture (Fig. 3). During the dry season, A_{sat} ($-8.4 \mu\text{mol m}^{-2} \text{s}^{-1}$) exceeded $\text{TER}_{\text{daytime}}$ ($3.5 \mu\text{mol m}^{-2} \text{s}^{-1}$) and light saturation was reached at approximately $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$, similar to the pasture. The highest LCP at the afforestation was observed during the dry-wet transition ($330 \mu\text{mol m}^{-2} \text{s}^{-1}$) and light saturation was reached at about $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$. During the wet season, the light response of NEE at the afforestation ecosystem was most pronounced with a low LCP ($189 \mu\text{mol m}^{-2} \text{s}^{-1}$) and the highest seasonal values of A_{max} ($-22.0 \mu\text{mol m}^{-2} \text{s}^{-1}$), A_{sat} ($-15.9 \mu\text{mol m}^{-2} \text{s}^{-1}$) and $\text{TER}_{\text{daytime}}$ ($6.1 \mu\text{mol m}^{-2} \text{s}^{-1}$). However, the light response during the wet-dry transition period was very limited and similar to the light response during the dry season.

Management controls of GPP and TER

Grazing. Grazing was the main management factor that influenced GPP and TER at the pasture site. Grazing varied substantially from June 2008 to January 2010, from zero to 75 livestock per day (median: 18.1) on the

6.5 ha pasture. This corresponds to a median and maximum of 1.6 and $8.0 \text{LU ha}^{-1} \text{d}^{-1}$, respectively (Fig. 4b). Periods of average grazing were constrained by isolated periods of overgrazing ($>4 \text{LU ha}^{-1} \text{d}^{-1}$). Lower stocking densities were observed in 2008 (median: $1.2 \text{LU ha}^{-1} \text{d}^{-1}$) compared with 2009 ($2.0 \text{LU ha}^{-1} \text{d}^{-1}$). On the other hand, periods of overgrazing persisted longer in 2008 (up to 9 days) compared with 2009 (up to 3 days).

Overgrazing strongly reduced GPP of the pasture ecosystem, particularly during the wet season 2008 (Fig. 1a). We observed a strong correlation between GPP and grazing intensity during the major part of the wet season 2008, with GPP being significantly reduced when the pasture was overgrazed. The significant reduction in GPP started immediately, reached a maximum after 4 days ($R^2 = 0.42$) of the start of overgrazing, and lasted for an average for 6 days. TER was reduced as well but was delayed with respect to the beginning of overgrazing. A significant reduction in TER started after 2 days, had its maximum after 6 days ($R^2 = 0.23$) and lasted on average for 9 days. Along with GPP, NEE showed less net uptake, which was most pronounced after 1 day ($R^2 = 0.37$) and lasted for 5 days. No significant time lag of GPP vs. grazing was observed during the wet season 2009. Furthermore, we observed an apparent reduction in ecosystem light response during and shortly after overgrazing: When excluding overgrazing periods with confounding limitations by environmental controls (namely PPFD), the pasture exhibited a reduction in daily photosynthetic capacity (A_{max}),

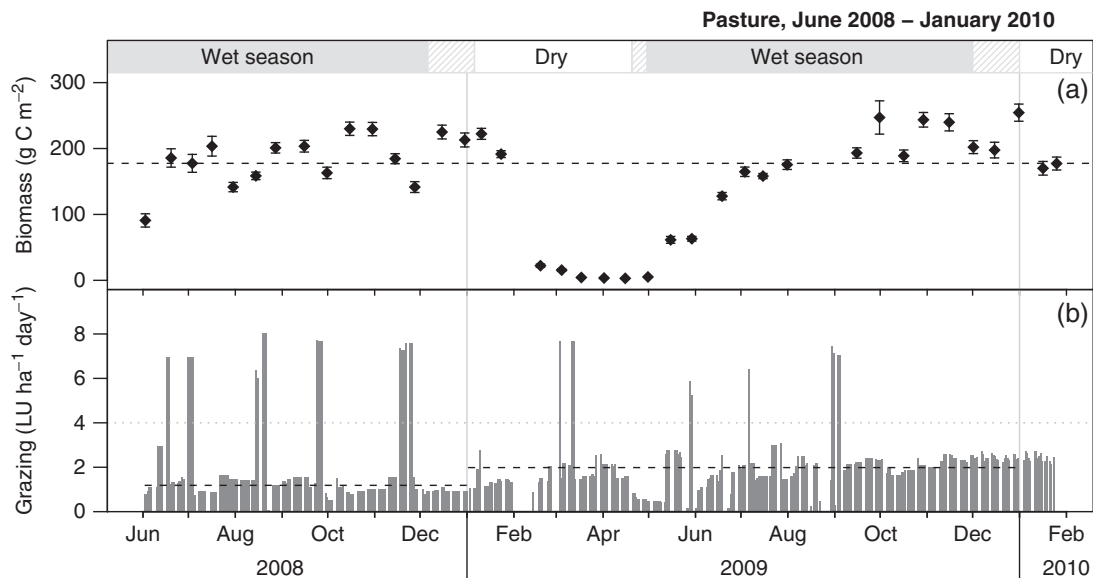


Fig. 4 Aboveground green biomass (a) and grazing (in livestock units, LU; b) at the Sardinilla Pasture from June 2008 to January 2010. The dashed black lines denote the overall median for biomass (a) and the annual median for grazing (b). The dotted grey line shows the overgrazing threshold of 4 LU.

increased TER_{daytime} and increased the LCP. For instance, during overgrazing in September 2008 (DOY 267–270, 7.7 LU ha^{-1}), A_{max} was reduced from 31.5 to $26.9 \mu\text{mol m}^{-2} \text{ s}^{-1}$, TER increased from 10.7 to $14.5 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and the LCP increased from 311 to a maximum of $597 \mu\text{mol m}^{-2} \text{ s}^{-1}$. We used this period of overgrazing combined with the reduction in aboveground biomass (DOY 259–274) and estimated an average forage consumption of $0.81 \text{ g C m}^{-2} \text{ d}^{-1}$ (for 1 LU) or $475 \text{ g C m}^{-2} \text{ yr}^{-1}$, when using the median stocking density of 1.6 LU ha^{-1} for Sardinilla.

Herbicide application. Another management factor at the pasture site was herbicide application by the farmer. The recovery of the vegetation after the dry season was dominated by the fast growing pioneering weed *Croton hirtus*, which inhibits the recovery of other grasses. In 2009, herbicide was applied by the farmer on June 1 and within about 2–3 weeks, the weed died off. Following the herbicide application, we observed a reduction in GPP by about 15%, an increase in TER by about 10% and a reduction in LAI from 2.75 ± 0.19 (June 8th) to 2.26 ± 0.15 (June 18th). No exact dates for herbicide application in 2007 and 2008 could be obtained.

Understory thinning. Thinning of the understory (weed removal) at the end of the year was the only management intervention at the afforestation site. No carbon was exported, and all clipped biomass was left on site. A major thinning (full afforestation area) was carried out in December 2007. This reduced GPP substantially by about 50% and turned the afforestation site into a carbon source (Fig. 1) for a period of 17 days. Understory thinning in December 2008 was minor and included only parts of the afforestation site. We observed an accompanying reduction in GPP as well but less strong than in 2007. This difference was largely due to lower TER in

December 2008. However, TER increased strongly following the thinning in 2008, indicating enhanced microbial activity due to decomposing litter.

Inventory data

Biomass. Significant seasonal variations in aboveground green biomass were observed at the pasture site, ranging from zero during the dry season and dry-wet transition period (senescent vegetation) to a maximum of 254 g C m^{-2} during the wet-dry transition period, with an overall median of $178 \pm 77 \text{ g C m}^{-2}$ (Fig. 4a). With re-growing vegetation after onset of the wet season, average aboveground biomass was reached during July and lasted until January, except for periods with pronounced overgrazing during the wet season 2008. Substantial reductions in aboveground biomass by up to 20% were observed following periods of overgrazing, e.g. in September 2008 from $204 \pm 8.9 \text{ g C m}^{-2}$ (DOY 259) to $163 \pm 8.7 \text{ g C m}^{-2}$ (DOY 274), when overgrazing occurred from DOY 267–270. Aboveground biomass and LAI were strongly correlated at the pasture site ($R^2 = 0.84$, $P < 0.001$). Belowground biomass was determined once in March 2009 ($n = 1$) and was with 176 g C m^{-2} similar to average aboveground biomass.

At the afforestation, total aboveground biomass more than tripled from $772 \pm 136 \text{ g C m}^{-2}$ in 2005 to $2449 \pm 891 \text{ g C m}^{-2}$ in 2009 (Table 3). Belowground biomass (coarse roots) increased from $112 \pm 63 \text{ g C m}^{-2}$ in 2005 to $693 \pm 306 \text{ g C m}^{-2}$ in 2009. In 2008, tree biomass (above and belowground) was the largest component of ecosystem biomass with $1533 \pm 705 \text{ g C m}^{-2}$ (72.3%), followed by understory vegetation with $546 \pm 89 \text{ g C m}^{-2}$ (25.7%), coarse woody debris (CWD) with $14.8 \pm 12.6 \text{ g C m}^{-2}$ (0.7%) and litter with $27.9 \pm 20.0 \text{ g C m}^{-2}$ (1.3%; Fig. 5). The annual increase in tree biomass was highest in 2006 (+69.4%) and 2009 (+66.6%), while it was smaller in 2007 (+55.9%) and

Table 3 Above- and belowground standing biomass at the Sardinilla afforestation from 2005 to 2009

	2005 (g C m^{-2})	2006 (g C m^{-2})	2007 (g C m^{-2})	2008 (g C m^{-2})	2009 (g C m^{-2})
Trees	299 ± 168	506 ± 269	792 ± 419	1116 ± 522	1861 ± 879
Herbaceous biomass	443 ± 109	401 ± 65	539 ± 82	546 ± 89	$546 \pm 89^*$
Coarse woody debris	2.1	21.8	18.3	14.8	14.8*
Litter	27.9 ± 20.0				
Total aboveground biomass	772 ± 136	957 ± 285	1377 ± 448	1705 ± 537	2449 ± 891
Roots	112 ± 63	190 ± 98	294 ± 144	417 ± 188	693 ± 306
Total biomass	884 ± 63	1147 ± 377	1671 ± 524	2122 ± 719	3143 ± 1189
Total biomass increment ($\text{g C m}^{-2} \text{ yr}^{-1}$)	–	263 ± 225	524 ± 275	450 ± 324	1021 ± 556

Values indicate mean \pm standard deviation. No data on herbaceous biomass and coarse woody debris were available for 2009 and thus, data from 2008 were used to estimate total biomass (*).

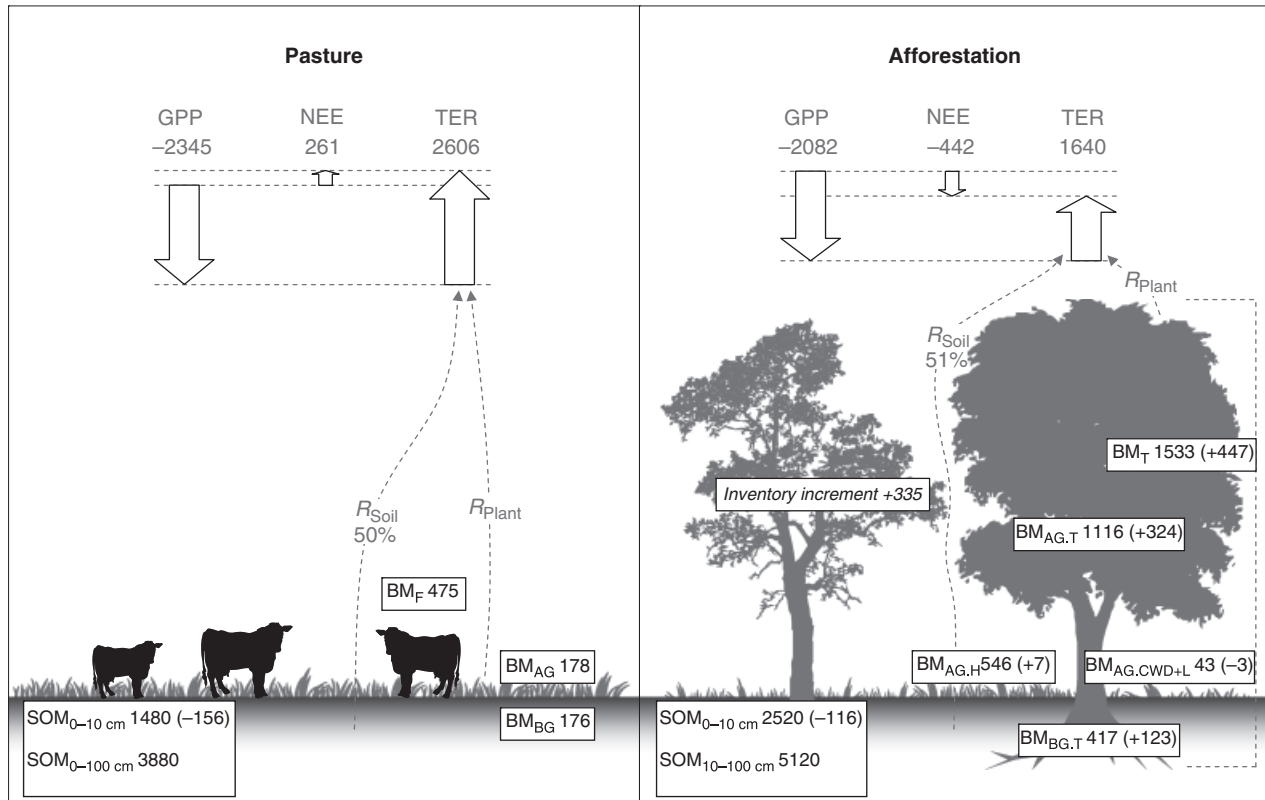


Fig. 5 Carbon stocks (g C m^{-2}) and fluxes ($\text{g C m}^{-2} \text{ yr}^{-1}$) in the Sardinilla pasture and afforestation in 2008. Grey numbers denote carbon fluxes with net ecosystem exchange (NEE) and its components gross primary production (GPP), and total ecosystem respiration (TER). Wide arrows indicate the size and direction of the fluxes, slim arrows the origin of the TER components soil (R_{Soil}) and plant respiration (R_{Plant}); the percentage denotes the measured source contribution of soil respiration. Numbers in boxes denote carbon stocks with annual increments ($\text{g C m}^{-2} \text{ yr}^{-1}$) given in brackets. Soil organic matter (SOM) is reported for topsoil (0–10 cm) and 10–100 cm depth. Aboveground biomass (BM_{AG}) in the afforestation is separated in tree biomass (BM_{T}), herbaceous biomass (BM_{H}), coarse woody debris (BM_{CWD}) and litter (BM_{L}). Belowground biomass (BM_{BG}) is reported for trees only, in the afforestation ($\text{BM}_{\text{AG,T}}$). In the pasture, foraged biomass (BM_{F}) by grazing livestock was estimated using the biomass reduction during periods of overgrazing. The 'Inventory increment' incorporates biometric uptake minus soil carbon losses.

lowest in 2008 (41.2%). The relative contribution of understory vegetation to the total aboveground biomass was reduced considerably from 50.1% in 2005 to 17.4% in 2009. However, total herbaceous biomass increased strongly from 2006 to 2007 (+34.5%), due to the invasion of *Saccharum spontaneum* (Canal grass) in parts of the afforestation site. Overall, annual ecosystem biomass increments varied strongly from $263 \pm 225 \text{ g C m}^{-2}$ in 2006, to a maximum of $1021 \pm 556 \text{ g C m}^{-2}$ in 2009. The large increment in 2007 was primarily associated with the strong increase in herbaceous biomass.

Soil. A strong reduction in topsoil (0–10 cm) carbon pools was found over a period of 8 years since 2001/2002 at both sites. This reduction was stronger at the pasture site (reduction of 1250 g C m^{-2} or -46%) as compared with the afforestation (930 g C m^{-2} or -28%,

Table 4). Correspondingly, nitrogen pools decreased more strongly at the pasture compared with the afforestation by 120 g N m^{-2} (-44%) and 80 g N m^{-2} (-30%), respectively. At the afforestation, the stable carbon isotope ratio ($\delta^{13}\text{C}$) became significantly more depleted from 2001 ($-17.0 \pm 0.8\text{‰}$) to 2009 ($-20.9 \pm 1.2\text{‰}$). This change in $\delta^{13}\text{C}$ indicated that in 2001 about 83% of the organic matter in the topsoil was derived from C_4 pasture vegetation, whereas this contribution had decreased to 57% by 2009. As expected, no significant change in $\delta^{13}\text{C}$ was observed at the pasture site. The total soil carbon pool from 0–100 cm depth was clearly lower at the pasture ($5.36 \pm 0.18 \text{ kg m}^{-2}$) than at the afforestation site ($7.64 \pm 1.63 \text{ kg m}^{-2}$). At both sites, roughly one-third of the carbon pool was concentrated in the top 10 cm of soil (27.6% and 33.0% for pasture and afforestation, respectively).

Table 4 Topsoil (0–10 cm) characteristics at the Sardinilla pasture (2002 to 2010) and afforestation sites (2001 to 2009)

	d_B (g cm ⁻³)	C (%)	C (kg m ⁻²)	N (%)	N (kg m ⁻²)	C:N	$\delta^{13}C$ (‰)
<i>Pasture</i>							
2002	0.86 ± 0.07	3.21 ± 0.45	2.73 ± 0.35	0.31 ± 0.05	0.27 ± 0.03	10.44 ± 0.70	-17.80 ± 1.86
2010	–	1.72 ± 0.33	1.48 ± 0.14	0.17 ± 0.04	0.15 ± 0.02	10.11 ± 0.16	-18.93 ± 0.56
<i>Afforestation</i>							
2001	0.59 ± 0.05	5.85 ± 0.52	3.45 ± 0.24	0.49 ± 0.03	0.29 ± 0.02	11.93 ± 0.68	-17.01 ± 0.78
2009	–	4.24 ± 0.92	2.52 ± 0.57	0.36 ± 0.08	0.21 ± 0.05	11.86 ± 1.32	-20.86 ± 1.23

Values indicate mean ± standard deviation. Bulk density (d_B), carbon concentration (C), carbon pool (C), nitrogen concentration (N), nitrogen pool (N), C:N ratio (C:N) and carbon isotope ratio ($\delta^{13}C$). Data from 2001/2002 are derived from Abraham (2004). Soil sampling at the pasture was done in January 2010 and at the afforestation in March 2009. No bulk density data were available for 2009/2010; hence, values from 2001/2002 were used to calculate soil pools.

Discussion

The pasture under investigation was heavily grazed at an intensity which cannot be considered sustainable under current conditions. In addition, water limitations led to strong and persistent carbon losses during the dry season that continued into the first weeks of the wet season. Due to overgrazing, carbon uptake of the pasture during the wet season was not sufficient to compensate carbon losses during the dry season. In contrast, the afforestation site persistently sequestered large amounts of carbon as measured with the eddy-covariance method and supported by biometric observations.

Environmental controls

The main environmental controls of ecosystem CO₂ fluxes in Sardinilla were PPFD and SWC. Considerable differences in the ecosystem response of pasture and afforestation to seasonal limitations in soil moisture were found, with the pasture ecosystem being more susceptible to seasonal drought than the afforestation. During the dry season, GPP at the pasture was strongly reduced whereas the afforestation maintained a GPP that exceeded TER well into the dry season (for about 75 days in 2008 and 81 days in 2009). This seems strongly related to the rooting depth of grasses vs. trees as we observed a mean rooting depth of only about 10–20 cm at the pasture. In comparison, mean rooting depth at the afforestation was 1.4 m in 2009 (Jefferson Hall, personal communication, unpublished data).

Light reduction due to cloudiness during periods of intense precipitation (e.g. in November) strongly reduced GPP at both ecosystems. Similar reductions in GPP were observed at tropical forest sites in Amazonia (Malhi *et al.*, 1998) and Costa Rica (Loescher *et al.*, 2003) during the wet season. However, the ecosystem response to varying light and soil moisture conditions

was very different between pasture and afforestation (Fig. 3). This seems predominantly related to the different photosynthetic pathways of C₄ grasses and C₃ trees. C₃ species are generally most active during the early growing season while C₄ species increase photosynthetic activity at warmer and drier conditions (Lambers *et al.*, 2008). An additional explanation for the limited light response of the afforestation during the wet-dry transition period could be the age of the foliage, as the chlorophyll concentration per unit leaf area decreases with age (Lambers *et al.*, 2008). It is likely that this is also the case with grasses but the grazed pasture vegetation has higher turnover rates and thus persistent re-growth of plant tissues.

GPP and TER patterns. Total annual GPP at the Sardinilla pasture was higher compared with the afforestation (Table 5) but lower than a tropical pasture in Brazil reported by Gilmanov *et al.* (2010) and Grace *et al.* (1998). Annual GPP at the afforestation was consistent with results reported by Vourlitis *et al.* (2001) for a transitional tropical forest in Brazil but lower than the range reported from tropical forests (Table 5). This is likely due to the young age of the afforestation, which is still in its establishment phase.

Overall higher TER in the pasture compared with afforestation (Fig. 5) seems to be caused by enhanced biomass turnover including decomposition rates due to grazing. The observed strong increases of TER during the dry-wet transition period are likely a combination of physical and physiological effects: Firstly, highly concentrated CO₂ is pushed out of the soil pore space (macro-pores and desiccation cracks; Birch effect). Secondly, large amounts of organic material that accumulated during the dry season start to decompose rapidly with the suddenly increasing soil moisture. The stronger increase in TER at the pasture compared with the afforestation seems related to additional accumulated organic material (manure) by grazing livestock.

Table 5 Summary of ecosystem CO₂ flux studies in the tropics

Site (Country)	Location (Lat., Long.)	Rainfall (mm yr ⁻¹)	Vegetation type	Time	LAI	TER _{night} (μmol m ⁻² s ⁻¹)	NEE _{day} (g C m ⁻² d ⁻¹)	GPP _{annual} (g C m ⁻² yr ⁻¹)	NEE _{annual} (g C m ⁻² yr ⁻¹)	Biomass (g C m ⁻² yr ⁻¹)	References
Xishuangbanna (China)	21°55'N, 101°16'E	1487	TMF	2003–2006	–	–	–	2594	–119	–359	Tan <i>et al.</i> (2010)
La Selva (Costa Rica)	10°26'N, 84°99'W	4000	TRF	1998–2000	2.7–4.9	7.05	–	3097	–242*	–	Loescher <i>et al.</i> (2003)
Sardinilla Afforestation (Panama)	9°18'N, 79°38'W	2267	P	2007–2009	1.2–2.9	6.5	0.5	2345†	261†	–	This study
Sardinilla Pasture (Panama)	9°19'N, 79°38'W	2267	YF	2007–2009	3.0–5.4	4.7	–1.0	2082†	–442	–450†	This study
Guyaflex (French Guiana)	5°17'N, 52°54'W	3041	TRF	2004–2005	6.9	10.0–15.0	–0.4	3911‡	–150	–102§	Bonal <i>et al.</i> (2006, 2008)
Caxiuanã (Brazil)	1°43'S, 51°28'W	2500	TRF	1999 (108 d)	5–6	7.6	–	3630	–560	–	Carswell <i>et al.</i> (2002)
Cuieriras, C14 (Brazil)	2°35'S, 60°07'W	2200	TRF	1995–1996	5–6	6.5	–	3040	–590	–230	Malhi <i>et al.</i> (1998, 1999)
Tapajos km67, Santarém (Brazil)	2°51'S, 54°58'W	1920	TRF	2002–2005	6–7	9.2	0.8	3157	94	200¶	Hutyra <i>et al.</i> (2007)
Ducke (Brazil)	2°57'S 59°57'W	2431	TRF	1987 (12 d)	5–6	5.95	–2.2	–	–220	–	Fan <i>et al.</i> (1990)
Tapajos km83, Santarém (Brazil)	3°3'S, 54°56'W	1920	TRF**	2000–2001	6–7	6.0–7.0	–	3000	130	200	Saleska <i>et al.</i> (2003)
Cotriaguacú (Brazil)	9°52'S, 58°14'W	2000	P–A	2002 (10 mo)	1.0–2.7	5.9	–4.6	–	–	–	Priante-Filho <i>et al.</i> (2004)
Jaru, Rondonia (Brazil)	10°05' S, 61°57'W	2170	TRF	1992–1993 (55 d)	4	6.6	–0.8	2440	–102	–	Grace <i>et al.</i> (1995, 1996, 1998)
FNS-A, Rondonia (Brazil)	10°46'S, 62°21'W	2170	P	1993 (11 d)	1.1–3.9	6.0	–1.9	4000	–	–	Grace <i>et al.</i> (1998)
		–	–	1999–2002	–	3.8	–1.8	–	–	–	von Randow <i>et al.</i> (2004)
		–	–	1999	–	–	–	3471	–400††	–	Gilmanov <i>et al.</i> (2010)
Sinop (Brazil)	11°25'S, 55°20'W	2037	TF	1999–2002	2.5–5.0	5.0	1.2	2062	–5	–	Vouritis <i>et al.</i> (2001, 2004, 2005)

Emendadas (Brazil)	15°33'S, 47°36'W	1556	S	1993–1994	0.4–1.0	4.8	–	–	–	–	–	–	–	–	–	–	–	Priante-Filho <i>et al.</i> (2004)
				2002 (10 mo)	2.5–5.0	3.9	–	–	–	–	–	–	–	–	–	–	–	<i>et al.</i> (2004)
				1993–1994	0.4–1.0	4.8	–	–	–	–	–	–	–	–	–	–	–	Miranda <i>et al.</i> (1996, 1997)
				1999–2000	–	7.6	–	–	–	–	–	–	–	–	–	–	–	von Randow <i>et al.</i> (2004)

All studies except the one from Xishuangbanna (China) were located in the neotropics. The vegetation types are tropical rainforest (TRF), Young forest (YF, <10 years), Transitional tropical forest (TF), Tropical forest with monsoonal climate (TMF), Pasture (P), Pasture with starting afforestation (P-A) and Savanna (S). Further listed are leaf area index (LAI), mean of nighttime total ecosystem respiration (TER_{night}), daily mean net ecosystem exchange (NEE_{day}), annual total gross primary production (GPP_{annual}), annual total net ecosystem exchange (NEE_{annual}) and total above and belowground biomass increment; except Guyaflux: only aboveground biomass increment. Missing information on location and climate was supplemented from the FLUXNET database (<http://www.fluxnet.ornl.gov>).

*Mean of 1998–2000.

†Values reported from 2008.

‡Reported by Gilmanov *et al.* (2010).

§Aboveground biomass of 70 g C m⁻² yr⁻¹ reported only, adding belowground estimate (45% of aboveground, (Malhi & Grace 2000) yields 102 g C m⁻² yr⁻¹).

¶Reported by Saleska *et al.* (2003).

||Derived from Table 1 in Malhi *et al.* (1998); modelled annual budget.

**Selectively logged in Sept. 2001 (reported measurements were done before).

††Estimated from Fig. 7f in Gilmanov *et al.* (2010).

Carbon budget synthesis. The pasture ecosystem was a large carbon source from 2007 to 2009. As far as we are aware, the average annual loss of 261 g C m⁻² yr⁻¹ is the first quantitative estimate for tropical pasture that covers more than 1 year (Table 5). Only three other studies reported total NEE, but on a daily base. All found carbon uptake for pastures: Grace *et al.* (1998) observed –1.9 g C m⁻² d⁻¹ in Amazonia during 11 days in May 1993, and von Randow *et al.* (2004) found similar uptake of –1.8 g C m⁻² d⁻¹ at the same pasture during 1999–2002. Priante-Filho *et al.* (2004) found an even larger carbon uptake of –4.6 g C m⁻² d⁻¹ in a pasture in conversion to afforestation.

The large carbon losses at the Sardinilla pasture could be either associated with soil carbon, dissolved organic carbon (DOC) or hidden abiotic factors like weathering of calcareous bedrock as suggested by Serrano-Ortiz *et al.* (2010). The substantial reduction in topsoil carbon seems to be the main source for the strong carbon losses (Fig. 5). Potential causes for the discrepancy to the EC measured carbon losses are measurement uncertainties or carbon export, such as by livestock or DOC. However, Waterloo *et al.* (2006) found that export of DOC played only a minor role in the carbon budget of a tropical forest with similar annual rainfall in Amazonia.

The seven-year-old Sardinilla afforestation was a larger net carbon sink in 2008 than reported for most tropical forests (Table 5). On the other hand, Carswell *et al.* (2002) and Malhi *et al.* (1998, 1999) found larger carbon sequestration while Saleska *et al.* (2003) and Hutrya *et al.* (2007) found carbon losses in tropical forests in Amazonia (Table 5). Consequently, the young afforestation is sequestering substantial amounts of carbon following its establishment phase that exceeds other, mature tropical forests. It can be expected that the carbon sink strength of the afforestation will continue and might even increase until the trees reach maturity (Canadell *et al.*, 2007), provided that there are no disturbances like fires, storms or harvesting. A long-term (55–61 years) inventory-based study of Silver *et al.* (2004) reported that carbon sequestration in a tropical afforestation did not slow down with aging trees, indicating significant carbon uptake (140 g C m⁻² yr⁻¹) even after the establishment phase.

Only few studies assessed comparative EC and biometric carbon budgets in the tropics (Table 5). In general, EC derived carbon budgets were lower than biometric field estimates as observed by, for example, Malhi *et al.* (1998, 1999) in Manaus (Amazonia), Saleska *et al.* (2003) and Hutrya *et al.* (2007) in Santarem (Amazonia), and Tan *et al.* (2010) in China (Table 5). The only tropical study that reported a larger carbon uptake with the EC method compared with biometric

data was Bonal *et al.* (2006, 2008) in French Guinea. Including the topsoil carbon losses with the biometric carbon uptake yields a similar result in Sardinilla, with a larger carbon uptake measured by EC compared with inventory data in 2008 ($-335 \text{ g C m}^{-2} \text{ yr}^{-1}$, Fig. 5). Only the study by San José *et al.* (2008) reported close agreement of EC and biometric-derived carbon budgets for a tall-grass *Andropogon* site and a savanna-woodland continuum in the Orinoco lowlands. However, and as emphasized by Saleska *et al.* (2003), large uncertainties are associated with both methods.

The change in topsoil $\delta^{13}\text{C}$ from 2001 to 2009 at the afforestation clearly indicates the increased inputs of organic matter (litter) by the dominating C_3 -vegetation in combination with the rapid carbon turnover in this tropical ecosystem. Besides the considerable reductions in topsoil carbon pools at both sites, it should be noted that topsoil generally constitutes only a small amount of the total soil carbon pool in the tropics. In Sardinilla, the topsoil carbon pool represents about 30% of the total carbon pool down to 1 m depth, which is more or less consistent with about 25% found for tropical forest at Barro Colorado Island (B. Turner, unpublished data).

Measurement uncertainties in the EC carbon budgets are largely related to ecosystem respiration and its consideration in data quality filtering and gap filling. We observed only a weak temperature sensitivity of nighttime ecosystem respiration, which is consistent with other tropical studies (Hutyra *et al.*, 2007) and the relatively low temperature sensitivity of tropical forest soils as reported by Davidson & Janssens (2006). Our results indicate that using weak temperature sensitivities to gap-fill nighttime ecosystem respiration could result in large biases of carbon budgets in tropical ecosystems. Hence, alternative running mean approaches should be considered more comprehensively. Further bias in carbon budgets can originate from advection (see e.g. Kruijt *et al.*, 2004). However, nighttime advection is probably only small at our Sardinilla. The u^* -filter and stationarity criterion used in data quality filtering are assumed to account for advection effects already (Aubinet, 2008; Etzold *et al.*, 2010). Further evidence for this is given by the energy balance closure, which was found to be comparable with other flux tower sites globally, with 84% and 81% for pasture and afforestation, respectively (Wolf *et al.*, 2011), and the close agreement with independently measured inventories.

Overall, the reported uncertainties in annual EC budgets range from less than $\pm 50 \text{ g C m}^{-2} \text{ yr}^{-1}$ for nearly ideal sites (relatively flat terrain) to ± 130 – $180 \text{ g C m}^{-2} \text{ yr}^{-1}$ for non-ideal sites with hilly topography (Baldocchi, 2003). Considering that both sites in Sardinilla are nearly ideal from a topographic perspec-

tive, we conservatively estimate that our annual budget uncertainties should be below $\pm 100 \text{ g C m}^{-2} \text{ yr}^{-1}$.

Management impact on carbon cycling. Both ecosystems exhibited strong responses to management, with understory thinning at the afforestation and grazing at the pasture site. Understory thinning considerably reduced GPP and gave evidence that understory vegetation accounts for a significant amount of GPP at the young afforestation 6–7 years after establishment. At the pasture site, periodical overgrazing during 2008 and persistently high stocking densities in 2009 were the major cause for carbon losses. Vegetation recovery was swift after periods of overgrazing during the wet season but was inhibited by soil moisture during the dry season. Hence, overgrazing during the dry season reduced aboveground biomass without the potential of recovery before the beginning of the wet season.

Similar rates of forage consumption by livestock like at the Sardinilla pasture were found by Dias-Filho *et al.* (2000) in the Amazon basin ($0.74 \text{ g C m}^{-2} \text{ d}^{-1}$). Wilsey *et al.* (2002) reported lower forage consumption at adjacent pastures in Sardinilla ($0.61 \text{ g C m}^{-2} \text{ d}^{-1}$) and found that grazing significantly reduced ecosystem respiration, but not carbon uptake. However, they also emphasized that grazing does not necessarily increase carbon losses from tropical pastures as the reduction in aboveground biomass lowers ecosystem respiration whereas grazing enhances aboveground productivity. Kirkman *et al.* (2002) reported a decrease in carrying capacity of about 50% from a cattle ranch in Brazil from 1992 to 2000, indicating a strong impact of grazing on carbon and nutrient cycling of tropical pastures. If the current losses in soil carbon and nitrogen continue, the pasture in Sardinilla seems at high risk of irreversible degradation. Consequently, a reduction of stocking densities to a maximum of 1 LU ha^{-1} appears crucial for mitigation efforts to decrease carbon losses in this highly seasonal climate.

Conclusions

We conclude that tropical afforestation can sequester large amounts of carbon, reduce the intra-annual variability of GPP, and enhance the ecosystem resilience to seasonal drought. High stocking densities in combination with seasonal drought can result in reduced productivity and carbon losses from tropical pasture. Projected changes in precipitation (reduction and increased variability) for Central America might affect the carbon balance of these tropical ecosystems in different ways, i.e., the carbon source strength of pastures might increase while the sink strength of afforestations might be reduced. Furthermore, the conversion from pasture to

afforestation may become more relevant for Panama and other Latin American countries in the future, within the carbon accounting of the Kyoto protocol.

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