A CASE STUDY OF CARBON POOLS UNDER THREE DIFFERENT LAND-USES IN PANAMÁ

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Abstract. This paper examines changes in carbon (C) pools associated with land-use, synthesizing data from two experiments dealing with different aspects of tree plantation establishment in Central Panamá. First, we analysed soil profiles in a grazed pasture and an adjacent 5-year-old teak (*Tectona grandis*) plantation. There were small differences in soil C mass in the top 10 cm of the pasture and the plantation, though analysis of paired profiles suggested larger differences at greater depth. Analysis of the δ^{13}C signatures in the pasture soils and litter showed that 90% to 95% of the organic matter in the surface 5 cm was derived from C_4 pasture plants, over the 45 years since the pasture was converted from forest. Comparison of the δ^{13}C signatures in the pasture and teak plantation profiles indicated substantial replacement of C_4—derived organic matter with the dominantly C_3—derived plantation tissues. Organic matter turnover times in the upper 10 cm of the soils ranged from 8 to 34 years and from 11 to 58 years in the upper 30 cm, depending on topographic location. We also present preliminary results, and technical challenges, for an eddy covariance experiment set up to provide a direct comparison between a grazed pasture and a native tree plantation. The two ecosystems studied are estimated to be small CO_2 sinks, 92 g C m^{-2} yr^{-1} for the pasture, and 57 g C m^{-2} yr^{-1} for native species plantation in the first year after establishment. The pasture's response to seasonal change was more pronounced, both in term of CO_2 fluxes and in term of herbaceous productivity, than the plantation's response. The storage below ground systems contained up 40% of the total sapling biomass.

1. Introduction

In the discussions around the Kyoto Protocol, opportunities for establishing significant carbon (C) sinks in the Tropics have been touted (IGBP Terrestrial Carbon Working Group, 1998). The Kyoto protocol clearly established a clause of "additionality", indicating that offsets can be claimed only for land C sinks induced directly by changes in human practices. Thus, in the context of managing the terrestrial biosphere to maximise C sequestration (Schulze et al., 2000), understanding the consequences of reforestation on ecosystem C storage becomes a necessity. Winjum and Schroeder (1997) suggested that a 11.8 Pg C stock could be credited to tropical plantations at the global level. Along the same lines, a report from the Royal Society (2001) suggests that tropical forestation, agro-forestry and regeneration together account for 39% of the potential for using land management as C

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sink to mitigate global emissions of CO_2. However, the result of a meta-analysis focussing on the impact of land-use change on soil C stocks suggest that the transition from pasture to plantation might in fact decrease soil C stocks (Guo and Gifford, 2002). House et al. (2002) examined the impact of future scenarios of complete reforestation and deforestation on atmospheric CO_2 concentration and concluded that the impact of land-use change will depend on the time course of fossil fuel emission. We adopted the view of Schopfhauser (1998) suggesting that "large-scale plantations are unlikely to quickly stabilize the carbon content of the atmosphere but could be part of a common strategy to solve the global emission problem."

We present a synthesis of experiments carried out in Panamá comparing C stocks in soil and plants associated with three land covers: grazed pasture and teak or native species plantations. Few studies have examined changes in soil C storage upon conversion of pastures back to forests or tree plantations, or of forests to tree plantations, even though this is a common phenomenon in many tropical regions (e.g. Montagnini and Porras, 1998). In the first series of experiments, we examined the impact of changes in land use from a tropical pasture to teak, *Tectona grandis*, plantation on different C stocks. We compare the soil properties of a grazed pasture with those found in an adjacent site that was converted to a teak plantation 5 years before the soil was sampled. We use δ^{13}C signatures of plant tissues, litter and the soil to quantify the turnover times and the changes in the origin of the soil organic matter induced by this land-use change. Ewell (1986) suggested that plantations would be more successful if they were designed to combine species with complementary resource utilization. We therefore became interested in studying the potential that native tree species represent in term of establishing C sink plantations. A permanent large-scale facility was established to study the links between biodiversity, land-use and ecosystem function. The site consists of 12 ha of forest plantation of six native tree species with two eddy-covariance towers measuring C fluxes over the plantation and an adjacent pasture (http://public.ornl.gov/fluxnet/siteplan.). Preliminary results from this experiment are presented and discussed.

2. Methods

2.1. Study Site

The bulk of results presented in this paper stems from experiments conducted in Sardinilla, Central Panamá (9°19′N, 79°38′W). Detailed description of the site and early land-use can be found in Wilsey et al. (2002). The field was a moist tropical forest, probably similar to Barro Colorado Island (9°09′N, 79°51′W) (Leigh et al., 1996) until logged in 1952–53, after which it supported 2 years of crops (e.g. corn, rice, plantain and yucca). The soil has been under pasture since then (40 to 45 years), with major species being, in decreasing order of abundance *Ischaemum indicum*, *Scleria malaleuca*, *Rhynchospora nervosa* and *Cynodon dactylon*. *I. indicum* and *C.*

dactylon are C_4 grasses while *S. malaleuca* and *R. nervosa* are C_3 sedges (Dahlgren et al., 1985). A topographically similar area 150 m southwest of the pasture was planted to teak (*Tectona grandis*) in August 1993 and has an understory of a C_3 shrub (*Fleminga strobelifera*) and the invasive C_4 grass *Saccharum sponteneum*. The area receives about 250 cm of precipitation annually, mainly in the rainy season from May to November when the monthly precipitation is about 25 cm. Mean annual temperature is 25°C and the site has an elevation of 70 m a.s.l. The soils are derived from Tertiary limestone and other sedimentary rocks. The upper slopes are covered with clayey Typic Tropudalfs and grade into clayey Aquic Tropudalfs in the lower slopes (Soil Survey Staff, 1990).

Two adjacent, relatively flat pastures were selected for the eddy-covariance experiment. One pasture was converted to the native species plantation in July 2001, while the other remains a grazed pasture. The plantation contained a mixture of six native tree species *Luehea seemanii*, *Cordia alliodora*, *Anacardium excelsum*, *Hura crepitans*, *Cedrela odorata* and *Tabebuia rosea*. After two growing seasons some trees reached 3 m in height and *H. crepitans* was reproductive (pers. obs). The experimental site provided two complementary methods to estimate the C storage potential of reforested plots, the compartment method consisting of measuring different components of C pools such as C in soil and in biomass, and a dynamic measure of C flows using gas-exchange.

2.2. SOIL SAMPLING AND ANALYSIS

A telescoping grid network was used for sampling the top 10 cm of the soils in the pasture. It comprised a 20 × 20 m grid, within which were nested one 5 × 5 m (covering 400 m^2) and one 1 × 1 m (covering 25 m^2) grids to define the small-scale spatial variability in soils. Samples were collected in June, 1998, at the start of the rainy season and after cattle had been excluded in May 1998; the field was generally lightly grazed. The top 10 cm was collected using a metal cylinder 5 cm in diameter, pushed into the soil surface, after removal of the litter. Because of the heavy texture of the soil, some compaction of the soil occurred in the cylinder, but this was mainly in the upper 5 cm and inspection showed that the full 10 cm were sampled. Two soil profiles to a depth of 1 m were sampled from the upper and mid parts of the field; samples were collected from the pit walls using the cylinder to allow estimates of bulk density. In the teak plantation, the 0 to 10 cm samples were collected at 20 m intervals on two perpendicular transects, along the crest and downslope, with a similar topographic position to the samples collected in the pasture. Two soil profiles were sampled in the same topographic position (upper and mid) as in the pasture.

Soils were analysed for field gravimetric and volumetric moisture content, bulk density, pH (in H_2O), loss-on-ignition (450°C for 16 hr) using standard methods (Carter, 1993). Organic C concentration was measured on a representative range of soil samples using an elemental analyser (Fisons Instruments model EA 1108) and a regression equation was developed to convert loss-on-ignition to organic C ($r^2 = 0.957$, $n = 32$). Litter from the pasture and plantation soils was collected from thirty 25 $\times$ 25 cm quadrats and oven-dried. Plant tissue, litter and soil samples were analysed for δ^{13}C. Soil samples were treated with 1 N. HCl to ensure removal of any carbonate, freeze dried and ball-milled to homogenise and litter and plant samples were ball-milled prior to analysis. Samples (2 to 4 mg) were analysed using an Isochrom Continuous Flow Stable Isotope Mass Spectrometer coupled to a Fisons elemental analyser (model EA 1108). Results were corrected to IAEA-CH6 (sugar), EIL-72 (cellulose) and EIL-32 (graphite). The δ^{13}C error for clean, ball-milled standard material was ± 0.2‰. Statistical characteristics of the surface soil properties were determined for the whole field at the 20 m scale and at the 1 and 5 m sampling scales.

2.3. EDDY COVARIANCE MEASUREMENTS OF CO_2 FLUX

Eddy covariance towers were installed in both a native species plantation and a grazed pasture in order to determine net ecosystem exchange (NEE). Fetch requirements have been estimated using a model of terrestrial diffusion (Horst and Weil, 1992, 1994; Kaharabata et al., 1997). The 150 m of available fetch has been verified to be sufficient in the pasture and in the plantation from pre-planting through year 5. Assuming an expected growth rate of 1 m per year, the available fetch will continue to be sufficient through year 10 for unstable and neutral conditions, but will begin to deteriorate for strongly stable conditions. Data acquired during periods of insufficient fetch will be omitted and replaced using data filling techniques. Criteria limiting the appropriate height of measurement over the plantation canopy have also been verified. The blending height, the height above which sub-plot heterogeneities are not observed (Claussen, 1989), will be roughly 3 m above the top of the canopy for all 10 yr of growth. Other criteria, the height of the interfacial sub-layer (Raupach, 1994) and the height of boundary layer distortion due to local micro-topography (Jackson and Hunt, 1975), are similarly less than 3 m above the canopy. Sensors will consequently be maintained at least 3 m above the canopy (Baldocchi et al., 1996).

Open-path eddy covariance systems have been employed, using the Campbell CSAT3 sonic anemometer and LICOR 7500 open-path IRGA. Data analysis includes methods of calibrated coordinate rotation (McMillen, 1988; Paw U et al., 2000), frequency corrections (Moore, 1986; Moncrieff et al., 1997), quality checking (Foken and Wichura, 1996; Vickers and Mahrt, 1997; Mahrt, 1998) and data filling. The sites have been instrumented for standard variables such as air temperature, humidity, rainfall, PAR, net radiation, soil temperature and soil moisture. The native species plantation has significant microtopography and has thus been additionally instrumented with topographically distributed soil temperature and soil moisture sensors within the tower fetch. Flux measurements began at the native species plantation in June 2001, more than 1 month before planting, to provide a baseline of the pre-planting condition and to observe changes during the act of planting. During a 1-week period in July 2001, two eddy covariance systems were operated in tandem at the native species plantation for an estimation of instrument uncertainty. Following this, the second system was moved to the pasture where data began in late-July 2001.

As an indicator of growth, height and basal diameter of all saplings were measured at the end of the first growing season (January 2002). In the first year of the study, the diameter of the saplings ranged from 1 to 69 mm and their heights ranged from 11 to 52 cm. Biomass was estimated by species-specific allometric regression equations (Potvin, submitted). To estimate herbaceous biomass, 96 quadrats (50 cm $\times$ 50 cm) were randomly positioned in the plantation and their vegetation was cut to ground level. The dry biomass was scaled up to estimate the total herbaceous biomass. The total biomass of the plantation was recorded, by calculating the sum of the average herbaceous biomass and of the sapling biomass. Herbaceous productivity was estimated by clipping the vegetation of 10 quadrats (50 cm $\times$ 50 cm) within each tower fetch at 4 months intervals throughout the year. Vegetation was allowed to re-grow for 2 weeks. It was then clipped again at soil level, oven dried and weighted.

3. Results and Discussion

3.1. EFFECT OF LAND-USE CHANGE ON SOIL C STORAGE

Average properties derived from the 128 soil samples collected from the pasture (0–10 cm) are pH 6.1, organic C concentration 5% and organic C mass 4 kg m^{-2}, with coefficients of variation (C.V.) of 0.066, 0.236 and 0.275, respectively. There was little decrease in the C.V. of pH and C concentration and mass as the sampling scale was decreased from 20 to 1 m (Table I). The surface soil properties are

TABLE I
Variation in mean and coefficient of variation (in parentheses) of surface soil properties 0 to 10 cm depth at sampling at scales of 1 (within 25 m^2), 5 (within 400 m^2) and 20 m (4 ha), with $n = 25$, 20 and 87, respectively

	Sampling scale (m)		
Soil property	1	5	20
pH	5.98 (0.03)	5.86 (0.04)	6.26 (0.07)
C content (%)	5.69 (0.25)	5.46 (0.16)	5.19 (0.26)
C mass (kg m^{-2})	3.75 (0.27)	3.64 (0.20)	4.01 (0.29)

similar to those reported by Yavitt (2000) for limestone-derived soils on Barro Colorado Island. Surface soil C mass changes associated with changes in land use are generally <50% in surface soils (0 to 10 cm depth) and <15% in the upper profile (0 to 30–40 cm) (see Murty et al., 2002), so considerable effort must be expended on sampling and analyses to adequately define the spatial variability and establish significant differences. The lack of a discernible spatial structure in soil properties in the Sardinilla pasture suggests that geostatistical techniques contribute little to a better understanding, or predictive capacity, in our system. Based on observed variability (Table I), the error of sampling at scales ranging from 1 to 20 m, with $n = 20$ to 87, would range from 1 to 5% of the mean for soil pH, but rise to 5 to 10% for organic C concentration and mass.

The soil profiles (1 m) at Sardinilla contained between 7.6 and 10.3 kg C m^{-2}. Jobbágy and Jackson (2000) estimated that the soils of the tropical deciduous forest biome contained an average of 15.8 kg C m^{-2} in the top 1 m, and those of the tropical grassland biome contained 13.2 kg C m^{-2}. These figures are larger than for the Sardinilla soils and part of the difference may be ascribed to differences in the depth distribution of organic C, resulting from inputs of soil organic matter from roots. In the Jobbágy and Jackson (2000) global data set, 33 to 36% of the soil organic C in the top 1 m was found in the upper 20 cm, and 56 to 59% in the upper 40 cm. In the Sardinilla soils, between 60 and 77% of the soil organic C to 1 m was found in the upper 20 cm, and 79 to 86% in the upper 40 cm. The greater concentration of organic matter close to the surface in Sardinilla may be related to: the limited rooting depth, the heavy clay texture, the relatively short dry season and the retention of soil moisture during the dry season (see Dietrich et al., 1996).

Surface soils (10 cm) in similar topographic positions (upper- and mid-slope) in the pasture and teak plantation revealed no significant change in organic C concentration and mass Table II). We observed, however, a significant decrease

TABLE II

Mean and standard error (in parentheses) of soil properties in top 10 cm for pasture and teak land uses, based on separation into upper- and mid-slope position ($n = 10$ to 19 for each position)

Soil property	Position	Pasture	Plantation
pH	Upper**	6.01 (0.08)	5.68 (0.06)
	Mid*	6.11 (0.09)	5.85 (0.10)
Org. C concentration (%)	Upper	5.33 (0.30)	4.79 (0.22)
	Mid	5.01 (0.42)	4.90 (0.22)
Org. C mass (kg m^{-2})	Upper	3.64 (0.22)	3.52 (0.20)
	Mid	3.61 (0.34)	3.74 (0.17)

Note. * and ** represent a significant difference at $p < 0.05$ and 0.01 levels, respectively (t-test).

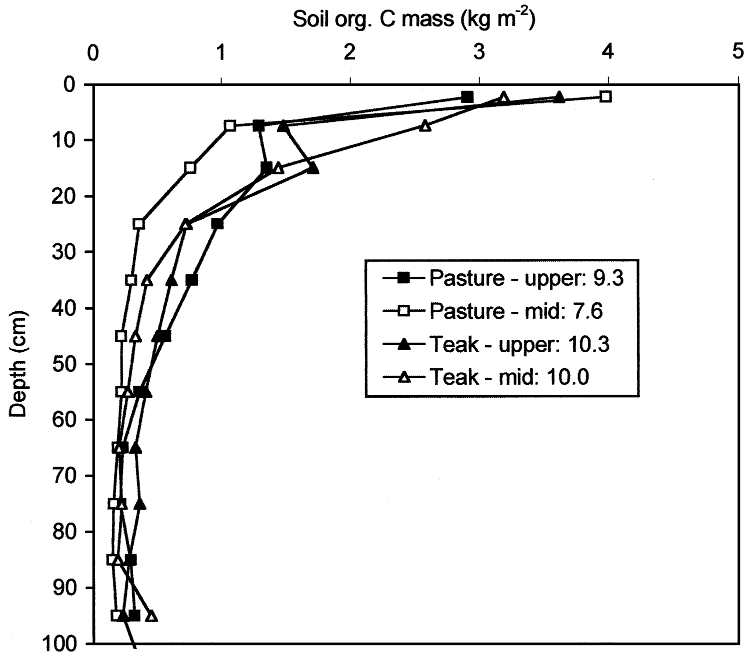

Figure 1. Soil organic C mass in upper- and mid-slope pasture and teak plantation profiles. (Figures in legend indicate mass down to 1 m.)

in pH from a mean of 6.0 to 6.1 (respectively upper and mid-slope positions) in the pasture to 5.7 to 5.9 in the teak plantation. Conversely, the upper- and mid-slope soil profiles in the teak plantation had larger organic C concentration and mass than those in the pasture (Figure 1). Assuming that the organic C mass was similar prior to land-use change, the profiles suggest an increase in organic C of 1.0 to 2.4 kg C m^{-2} in the 5 years since land-use conversion, of which 0.9 and 0.7 kg C m^{-2} occurred in the top 10 cm. This illustrates the danger of relying on few measurements from soil profiles compared to sampling more intensively in the surface soil layers.

The detection of changes in the organic C of soils is dependent on either being able to monitor the C pool through the land-use change, or to establish sites whose soil properties were the same prior to the change. The differences in isotopic signature of plant, litter and soil organic C provide a powerful tool to identify changes in the origin of soil organic matter, even though the amount of organic matter may show a small change. In Sardinilla, the pasture is dominated by C_4 grasses, *Ischaemum indicum* being the most abundant species (Wilsey et al., 2001). Soil δ^{13}C values in the pasture were about −15‰ in the surface 5 cm and became more negative with depth, reaching values of −18 to −20‰ below 50 cm (Figure 2). Data on δ^{13}C composition of the original forest soils and vegetation are not available, but tropical rain forest vegetation usually has δ^{13}C values in the range of −30 to −33‰

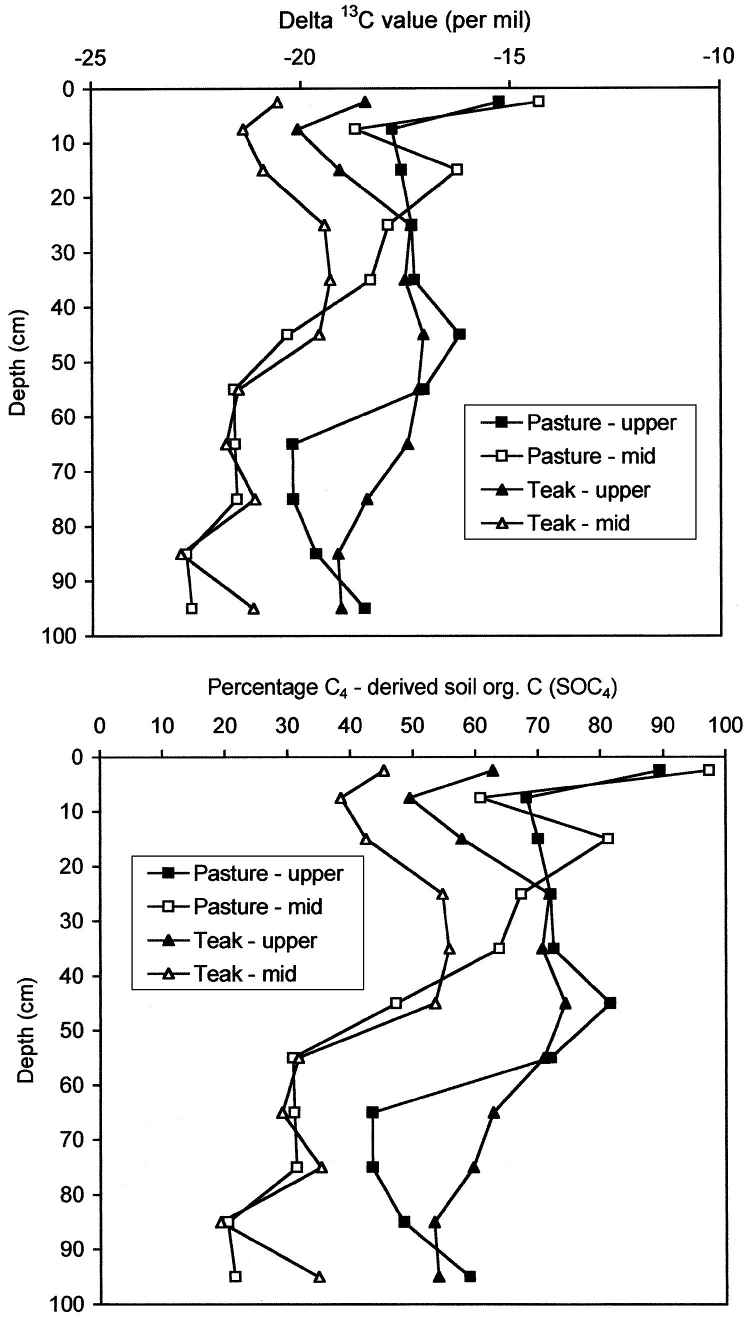

Figure 2. δ^{13}C value (upper) and percentage of soil organic C (SOC_4) derived from C_4 plants (lower) in upper- and mid-slope pasture and teak plantation profiles.

(e.g., Martinella et al., 1998). Fractionation during plant tissue conversion to soil organic matter results in tropical forest soil profiles with $\delta^{13}C$ values of between -25 and -27‰ (e.g., Bashkin and Binkley, 1998; Veldkamp, 1994; van Dam et al., 1997).

To estimate the origin of the soil organic matter, we assumed (1) that the original forest profile had a $\delta^{13}C$ value of -26 and -25‰ in the 0 to 50 and 50 to 100 cm depths, respectively, and (2) that the pasture added organic matter with a $\delta^{13}C$ value of -14‰ (Table III). The proportion of soil organic C derived from C_4 plants (SOC_4 see Bashkin and Binkley, 1998) in the two pasture profiles ranged from 90 to 95% in the surface 5 cm and decreased with depth (Figure 2). In the upper-slope soil profile, SOC_4 remained between 70 and 80% from 10 to 50 cm and then fell to less than 50% in the lower part of the profile. In the mid-slope profile, the decline in SOC_4 content was more rapid, with 20 to 35% reached below 50 cm. For the 1 m of soil profile, it can be estimated that 2.4 to 4.0 $kg\,C\,m^{-2}$ was derived from the original forest and 6.3 to 6.9 $kg\,C\,m^{-2}$ from the pasture vegetation. Between 75 and 78% of the current soil organic matter is derived from pasture and crop inputs in the past 45 years.

TABLE III

$\delta^{13}C$ values of above-ground plant tissues and litter in the pasture and the teak plantation. Litter samples are composites of individual samples (25 × 25 cm) collected within the topographic positions

Material	$\delta^{13}C$ (‰)
Plant Species	
Pasture	
Ischaemum indicum	−11.6
Rhynchospora nervosa	−28.6
Teak plantation	
Teak (*Tectona grandis*) leaves	−28.8
Fleminga strobelifera leaves	−33.2
Saccharum spontaneum	−12.7
Litter	
Pasture	
Upper slope	−14.0
Mid slope	−13.9
Lower mid slope	−14.0
Lower slope	−13.4
Teak plantation	
Upper slope	−25.6
Mid slope	−27.4

In the teak plantation soil profiles, $\delta^{13}C$ values were about −18 to −21‰ in the surface 20 cm and remained between −17 and −22‰ through the lower part of the profiles (Figure 2). Composite litter samples from the teak plantation floor revealed average $\delta^{13}C$ values of −26 and −27‰ from samples taken from the upper- and mid-slope positions, respectively (Table III). Repeating the methodology used in the pasture, the proportion of soil organic C derived from C_4 plants (SOC_4) in the teak plantation soil was 45 to 63% in the top 5 cm and decreased to 38 to 50% at 5 to 10 cm. The proportion then increased to 50 to 70% in the middle part of the profile, before reaching values of 55 to 70% and 20 to 55% in the lower part, similar to that found in the two pasture soils (Figure 2). These results suggest that there has been a substantial replacement of SOC_4 by SOC_3, particularly in the upper part of the teak plantation profiles. SOC_4 mass has declined by 0.5 to 2.1 kg C m^{-2} in the top 10 cm and by 0.4 to 1.9 kg C m^{-2} in the top 30 cm, representing decreases of 9 to 46% of the original, pre-plantation SOC_4 mass. Thus, although the total organic C mass has increased after land-use conversion, by 1.0 to 1.8 kg C m^{-2}, the SOC_4 mass has decreased. This represents an increase in plantation-derived SOC_3 of 1.4 to 3.6 kg C m^{-2} over the 5 years, an average of 0.3 to 0.7 kg C m^{-2} yr^{-1}.

The changes in soil C brought about by the land-use conversion, based on the comparison of paired profiles and surface sampling, are questionable. It cannot be proven that the soil profiles were identical before land use changed and the data on subsoil pH and bulk density suggest that they may have been different before land-use change. It is clear, however, from the isotopic analysis that there is a rapid turnover of organic matter in these systems. The turnover time of the SOC_4 fraction can be calculated from the mass lost through conversion of pasture to plantation. Losses of 14 to 46% SOC_4 in the 0 to 10 cm depth and 9 to 36% in the 0 to 30 cm depth represent estimated turnover times of 8 to 34 and 11 to 58 years. The mid-slope soil also appeared to have gained more organic C and lost a higher proportion of its SOC_4 than the soil on the upper slope. If the soil C content in the initial forest was the same as in the current pasture and derived entirely from C_3-plants, then the turnover time of organic matter since conversion from forest 45 years ago would be 30 and 18 years, for upper- and mid-slope soils, based on the current proportion of SOC_3 in the soil profiles. These turnover time estimates are similar to the range calculated for tropical soil land-use change by Giardini and Ryan (2000).

3.2. PRELIMINARY CO_2 FLUX AND PRODUCTIVITY DATA

Flux data suggest that, contrary to our expectation, the disturbance caused by tree planting did not induce the new plantation to become a source of CO_2 (Figure 3). Site preparation and planting were conducted throughout the month of July 2001, but the plantation sink dipped only slightly during that period and quickly recovered to a constant level for August to October. In fact, the sink in the following July 2002 is lower than during the planting month of July 2001. Over the first year of

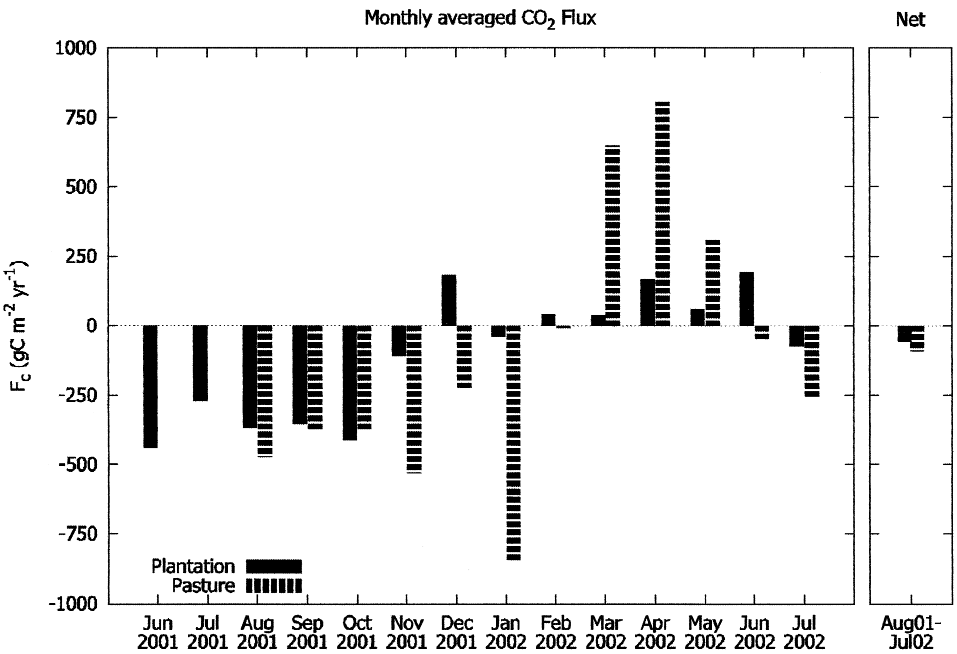

Figure 3. Monthly averaged CO_2 flux and net annual flux, Sardinilla Carbon Project Plantation and Pasture, June 6, 2001 to July 31, 2002. Net flux is for August 1, 2001 to July 31, 2002.

the experiment, the two ecosystems studied are estimated to be small CO_2 sinks, 92 g C m^{-2} yr^{-1} for the pasture, and 57 g C m^{-2} yr^{-1} for native species plantation in the first year after establishment. At this early stage, the total biomass of the plantation was largely dependent on the herbaceous biomass. In January 2002, the saplings' biomass made up some 0.72% of the total biomass reaching an average height of 52 cm. The two ecosystems showed different seasonal patterns with more fluctuations in gas exchange in the pasture than in the plantation (Figure 3). Differences in December and January coincide with the transition from wet to dry season. Flux data suggest that the plantation switches to a source during a cloudy December, while the pasture is able to maintain a sink and recover with a substantial sink in January since there was sufficient soil moisture until late in the month. In the dry season, the native species plantation is a small source of CO_2 but a much larger source in the grazed pasture. There is good agreement between the patterns detected by the flux towers and our measures of herbaceous productivity. Productivity data (Figure 4) showed stronger seasonal patterns in the grazed pasture than in the plantation. During the wet-dry transition, productivity decreased by 47% under the plantation tower in contrast with a 75% reduction under the pasture tower. In Sardinilla, the rainy season starts to establish in April. Productivity increased by 44% under the plantation tower and by 95% under the pasture tower. These preliminary results suggest that flux data and biomass pool estimates can be useful complementary methods to understand patterns of C cycling.

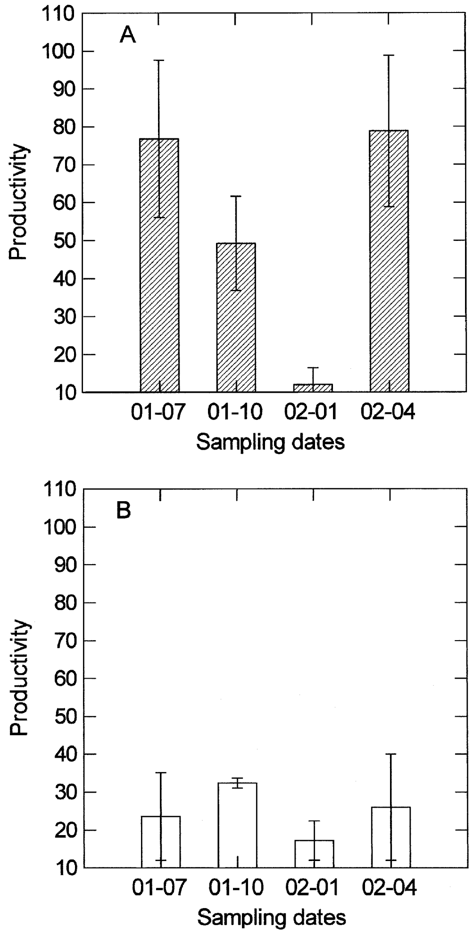

Figure 4. Productivity estimates (g $*$ m^{-2}) under (A) the pasture tower and under (B) the tower established in the native species plantation. Sampling dates were July and October 2001 as well as January and April 2002 and span the first year of the plantation.

The first year of running two flux towers in Sardinilla yielded significant practical experience for flux measurement in the tropics. We recommend saving raw eddy covariance data for as long as possible, or at least long enough to define aspects of the site. There is still no consensus as to a definitive set of analysis methods, and raw data are necessary for reprocessing should these methods change. Raw data are also necessary to define peculiarities of the site or instrumentation, including: nighttime wind regime, susceptibility to time series spikes/shifts, and anemometer directional bias (calibrated coordinate rotation). Since two flux towers were available for this experiment, it was possible to run two identical sets of equipment for a 1-week period. This period was invaluable for confirmation of analysis techniques, and found uncertainties in fluxes to be 8% for sensible heat, 1.5% for latent heat and

6% for CO_2. The primary challenge in measuring flux at Sardinilla has been a lack of sufficient turbulence at night. In the first year, only 28% of night data points in the plantation had average wind speeds above 1 m s^{-1} and only 7% were above 2 m s^{-1}. The more sheltered pasture was even worse with 10% above 1 m s^{-1} and less than 1% above 2 m s^{-1}. Therefore, we developed a novel sectioning and detrending method (ARMA detrending) that increased the night-time data set to 30%. The daytime data set is also increased from 54% to 72% by these methods, effectively including daytime points under transitional or marginal cloudy conditions. Following this procedure of recovering an acceptable amount of the raw data, seasonal and annual trends can be observed with more confidence.

3.3. WHOLE ECOSYSTEM C STORAGE

Our experiments emphasise the importance, for young tropical plantations, of the carbon pools located below ground either in the soil or as coarse roots. More than half of the C sequestered by the 5-year-old teak plantation is found below ground, mostly as soil C (Table IV). In a companion study on four mature teak plantations planted in 1978–1979 near Sardinilla (Kraenzel et al., 2003) showed that two-thirds of C storage took place below-ground (on average 19.9 of 30.7 kg C m^{-2}). At the ecosystem level in both young and mature teak plantation, soil and root biomass, therefore represent the most important C pools. We also examined the below-ground biomass allocation of native tree species. Across species, mean root allocation was 28.5% ± 6%. We observed significant variation in root allocation

TABLE IV
C pools (kg m^{-2}) associated with pasture to teak plantation land-use change

Component	Pasture	5-year-old teak	20-year-old teak
Biomass[a]	0.25	2–3	12.1
Litter	0.12	0.24	0.27
Soil[b] 0–10 cm	3.63	3.63	n.a.
Soil[c] 0–10 cm	4.7	5.6	
Soil[c] 0–30 cm	6.4	7.7	
Soil[c] 0–100 cm	8.5	10.2	18.3
Total ecosystem[c]	9.0	13.0	30.7

Note. Data from Sardinilla are for a pasture and a teak plantation after 5 years (mean of upper- and mid-slope locations). Data from 20-year-old plantations are the average of four plantations in Central Panamá (Kraenzel et al., 2003). Note that the soil profile for the 20-year-old plantation goes down to 130 cm rather than 100 cm.
[a]Estimated from Wilsey et al. (2002), Kraenzel et al. (2003) and Hase and Foelster (1983).
[b]Based on grid soil sampling.
[c]Based on paired soil profiles.

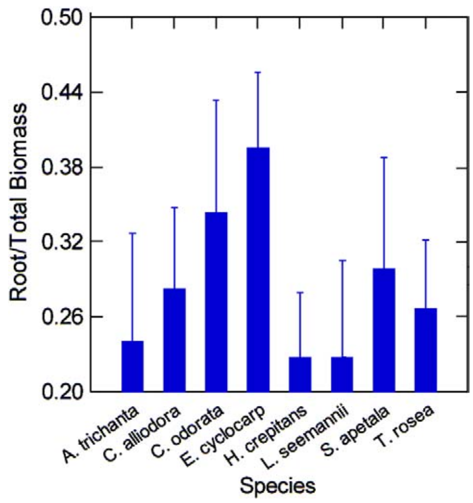

Figure 5. Root: total biomass ratio for 8 native tree species grown in Sardinilla for 3 years. Species are *Luehea seemannii*, *Cordia alliodora*, *Sterculia apetala*, *Antirrhoea trichantha*, *Enterolobium cyclocarpum*, *Cedrela odorata*, *Tabebuia rosea* and *Hura crepitans*. (Details on methodology in Potvin (submitted).)

between species ($F_{7,32} = 3.5$, $p < 0.001$). Our data show that roots can account for as much as 40% of the total biomass of 3-year-old saplings (Figure 5). Root biomass data can be aggregated to provide estimate of the below ground biomass pools of forests. Sanford and Cuevas (1996), in a compilation of data from some tropical forests world-wide, reported that below-ground biomass accounted for 87.9% in Venezuela for forests established on Spodosol but only 1% for riparian forests of Panamá. The authors suggested that variation in root biomass, at the forest level, might be controlled by soil texture and quality.

Some assessment of the relative significance of different C pools within the overall ecosystem with changes in land cover is found in Table IV. Wet-season biomass in the pasture was estimated at 0.25 kg C m^{-2}, compared to between 2 and 3 kg C m^{-2} in the 5-year-old teak plantation; mature teak plantations contain up to 12 kg C m^{-2}. Litter mass in the pasture was about half that found in the teak plantation (0.12 and 0.24 kg C m^{-2}, respectively); undisturbed forests at Barro Colorado Island contain 0.3 to 0.4 kg C m^{-2} in litter (Wieder and Wright, 1995). Thus, in five years, land-use change brought about an increase of 2 to 3 kg C m^{-2}, or an average of 0.4 to 0.6 kg C m^{-2} yr^{-1} in plant biomass and litter. The profile soil sampling for the pasture and 5-year-old plantation suggested that the C content of the teak plantation soils may have increased, on average, by 0.9 kg C m^{-2} in the top 10 cm and 1.3 kg C m^{-2} in the top 30 cm, and 1.7 kg C m^{-2} in the top 100 cm.

An increase of such a magnitude in soil C in the teak plantation is surprising given the observed litter and biomass production. Yet the rapid rate of incorporation of C into tropical soils might find an echo in the data from the 20-year-old plantations. The soil profiles of the four mature teak plantations were sampled to a depth of 2 m and the average profile C storage was high, 22.4 ± 9.8 kg C m^{-2} (Kraenzel et al., 2003). Caution is necessary in the interpretation of the data from the mature teak plantations as we do not have a good history of land-use for them. Most studies of land-use change have, likewise, used a paired site approach, in which assumptions are made about the similarity of the systems prior to land-use change without really being able to confirm the assumption. Our concern over the interpretation of comparative land-use studies played a central role in the development of the native tree reforestation experiment. A fundamental contribution of the Sardinilla experiment was to adopt an experimental design allowing to evaluate directly the changes in C fluxes and pools through time. We are combining a variety of approaches, from paired site to a time sequence of flux measurements, to examine changes in various C pools associated with reforestation. In the case of our multi-species plantation, we expect the changes in C pools above ground to be large, and therefore easily detectable and our preliminary data suggest that the time-integrated NEE of the pasture and plantation already differ 1 year after planting.

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