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Carbon stocks and fluxes in a temporal scaling from a savanna to a semi-deciduous forest

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Abstract

The strength of carbon sink and stock was assessed in a protected savanna of the Orinoco Llanos by the harvesting plant phytomass and using allometric relationships between the dry mass and the censuses of plant height. Thus, changes in the carbon stock and the proportion in the tree/grass proportion were evaluated throughout age states. Results indicate that the carbon stock in the vegetation increased from 207 to 9215 g C m^{-2} whereas in the soil, it varied 6680 to 12 196 g C m^{-2}. The carbon stock accumulation was mainly related to increases in the woody layer from 36 to 9215 g C m^{-2} (255-fold) and in the soil from 1341 to 12 196 g C m^{-2} (nine-fold), respectively. The estimated pool of carbon sequestered in the Orinoco Llanos by the restored forest in 51 years was 5.69 Pg C. The expansion and conservation of this carbon pool might remove CO_2 from the atmosphere to help compensate for CO_2 liberation associated with other land uses or industrial practices. © 1998 Elsevier Science B.V.

Keywords: Carbon cycles; Carbon sequestering; Climatic changes neotropical savannas; Orinoco Llanos

1. Introduction

Savannas are characterized by a wide range of physiognomic types, which primarily reflect variation in tree cover and density (San Jose and Montes, 1991). The balance between tree/grass components is dynamic and a function of the complex interaction of climate, soil, water availability and disturbance (Whittaker, 1975; Walker and Noy-Meir, 1982; Cole, 1986; Yeaton, 1988; Skarpe, 1991, 1992). Grass-dominated vegetation, including savannas, covers 20 to 30% (1500×1012 m^2) of the terrestrial biosphere (Pemadasa, 1991; Werner, 1991). As a result, this vegetation type has the potential to influence the global carbon budget.

Humans have a history of influencing the tree/grass balance in neotropical savannas dating back to the last glaciation (Wijmstra and van der Hammen, 1966; van der Hammen, 1992). Recently, the impact of human activity on savannas has increased due to demographic and economical pressures (Young and Solbrig, 1993). Predictions indicate that the savanna human population, now calculated to be in one-fourth of the world's population, will increase significantly in the near future (Scoones

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et al., 1993). Much of the land has been converted into forestal plantations or developed for intensive agriculture and pasture. In addition, intensive petroleum extraction and refining activities in the Orinoco Llanos, where the petroleum belt covers over 25% of the whole area, released on estimated 0.057 Pg C yr^{-1} in 1990. This is equivalent to 6% of the total carbon emission in the northern of the Orinoco Llanos (MARNR, 1995). Together, these changes in savanna land use have the potential to influence global biochemical.

Neotropical woody vegetation has been cleared and opened by fire yielding wide-spread savannas in the tropical zone (San Jose et al., 1991). The annual rate of conversion of tropical grassland to agriculture is 0.0033×10^{12} m^2 yr^{-1} and the annual deforestation is 1.7% (FAO, 1983). The human impact on this vegetation has released a significant magnitude of CO_2, due to changes in soil carbon associated with harvested wood and the increase in cultivated areas. Conversion of tropical forest to permanent agriculture and grazing lands has reduced the carbon density by 40%; whereas conversion to pasture has reduced the carbon content by 20% (Detwiler and Hall, 1988a,b). In the neotropics, the net release of carbon to the atmosphere due to deforestation ranged from 0.20–2.5 Pg C yr^{-1}; particularly the grazing systems released 0.046 Pg C yr^{-1} (Molofsky et al., 1984; Detwiler et al., 1985; Detwiler and Hall, 1988b; Hao et al., 1990; Houghton, 1991b). Houghton et al. (1987) have reported that for 1980, approximately 80% of the net carbon flux from biota (1.8 Pg of C yr^{-1}) is associated with change in land use in the tropics.

The net balance between carbon sinks and sources in the savanna region as well as the management of the size and nature of sinks to control the greenhouse effect have been predictively modelled by several authors (Emanuel et al., 1985a,b; Keeling et al., 1989; Tans et al., 1990; Burke et al., 1991; Schimel et al., 1990; Mosier et al., 1991; Ojima et al., 1993; Taylor and Lloyd, 1992; Parton et al., 1995). However, there is scarce information on the savanna carbon budget.

The aim of this work is to temporarily assess the strength of a protected neotropical savanna as a carbon sinks in the Orinoco Llanos. In this protected savanna, allometric relationships between the dry mass of the individual trees species and plant height were used for scaling the temporal variation in the carbon proportion of the tree/grass components. Probable consequences of the change in the savanna carbon budget are analyzed.

2. Materials and methods

2.1. Study site

The area was located at the Biological Reserve, Calabozo, Venezuela (8°56′N; 76°25′W). The landscape of the study site is an alluvial highland formed from detrital material (alluvial cones and deltaic deposits), accumulated during lower Pleistocene in the Mesa formation (Hedberg and Pyre, 1944). The soil was classified as Haplustox according to the US Soil Taxonomy System (Soil Survey Staff, 1975).

The vegetation growing season occurs from April to November with 98% of the annual precipitation (1249 mm). The studied area presents a megaisothermal climate with monthly mean temperature ranging from 29.0 (April) to 26.7°C (December). This small annual variation contrasts with the daily oscillation, which ranges from 10 to 15°C. Annual pan evaporation was 2210 mm, which reflects a proportion of 2:1 in comparison with the rainfall data.

The vegetation is a closed bush island savanna (Hill, 1969), consisting of isolated patches of semi-deciduous forest (San Jose et al., 1978). Characteristic species of the upper stratum (12–25 m) were *Cassia moschata*, *Hymenaea courbaril* and *Copaifera publiflora*. A second stratum (5–12 m) was characterized by *Lonchocarpus ernestii*, *Luehea candida*, *Pterocarpus podocarpus*, *Fagara caribaea*, *Vochysia venezuelana*, *Cochlospermum vitifolium* and *Godmania aesculifolia*. The inconspicuous shrub stratum (2–5 m) was dominated by *Chomelia spinosa*, *Erythroxylum orinocense* and *Randia aculeata*. A discontinuous herbaceous stratum included *Xanthosoma helleborifolium*, *Caladium bicolor*, *Bromelia chrysantha* and *Ruellia paniculata*. Plant names follow the nomenclature Venezuelan National Herbarium.

The patches of semi-deciduous forest are vegetation remnants, which are protected by chance. They occupy an area usually < 12 m in diameter, although this may sometimes increase to 1 ha or more.

One of the main reason for their permanence is the belt of fire resistant species, such as *Curatella americana*, *Bowdichia virgilioides* and *Byrsonima crassifolia*, that surrounds the edge of the patches that act as firebreaks and thus, provide fire protection to seedlings.

2.2. Census of vegetation

Temporal changes in carbon stock were assessed in a 3 ha permanent plot, which was protected from fire and cattle grazing. This method is the more reliable for studying vegetational changes (Mueller-Dombois and Ellemberg, 1974; Austin, 1981; Kent and Coker, 1992). Thus, the 3 ha-plot was censused periodically for tree density in 1961 (Blydenstein, 1963), 1969 (San Jose and Fariñas, 1971), 1977 (San Jose and Fariñas, 1983) and 1986 (San Jose and Fariñas, 1991). The initial stage of this plot representing a burned savanna with grass dominated cover and few scattered trees served as a control or baseline from which were compared and evaluated changes in the protected savanna. The vegetational trend observed in this plot (San Jose and Fariñas, 1991; San Jose et al., 1994) indicate that after 25 years of protection, the savanna is changing toward a woodland vegetation, which is similar to the patches of semi-deciduous forest found in the annually burned savannas. Therefore, the vegetational sequences inferred from the protected plot was completed by including the largest semi-deciduous forest found in the Biological Reserve.

The tree density trend observed in the protected plot toward the semi-deciduous forest was assessed in terms of the standing crop using a dimension analysis consisting of the allometric relationships between the aboveground dry mass of individual tree species and plant height. Censuses of plant height were taken in the protected plot at the assumed age states (1961, 1964, 1977 and 1986) by recording individuals of each species and numbering all stems above or equal to 0.05 m. Since some new tree species have spread vegetatively, it was impossible to determine whether new individuals were the results of new seed establishment or vegetation propagation of existing trees. Therefore, we will refer to them as tree stems or stems. Structure and description of the studied vegetations were given elsewhere (Montes and San Jose, 1995). The largest forest patch of semi-deciduous forest (1.3 ha) was selected at the Biological Reserve and all the stems (≥ 5 cm height) were counted during 1991 as described above.

2.3. Determination of the carbon stocks in the vegetation and soil at the assumed age states

2.3.1. Woody component

2.3.1.1. Aboveground carbon stock. Allometric relationships. Allometric relationships have been used for determinations of the standing crop in a wide range of woody vegetations. A review on this methodological approach was outlined by Whittaker and Mark (1975), Brown et al. (1989), Kauppi and Mielikaimen (1992) and Wofsy et al. (1993). Thus, height/biomass relationships were determined for each tree species found in the studied savannas. The full range of heights represented in stands was sampled for 0.5 m height increments by felling 40 trees per height class. The trees were selected at random in protected and burned savannas, including scattered individuals in the herbaceous layers as well as trees growing in the semi-deciduous forest patches. Leaves, branches and stems were weighted, and subsamples were oven-dried at 80°C until constant dry mass. Whole plant fresh weights were then converted to dry weight based on these fresh/dry weight ratios from subsamples.

2.3.1.2. Belowground carbon stock. In the study plots in Section 2.3.1.1, the number of soil plots needed for 20% precision in the belowground carbon stock determinations was assessed (Sokal and Rohlf, 1981) using the following procedure. Plots of 25 m^2 each were randomly selected for among those when trees had been harvested. The soils were excavated at 0.1 m increments to 0.3 m depth. Soil samples from 0.0 to 0.3 m depth contained more than 85% of the tree belowground dry mass up to 2 m soil depth (San Jose et al., 1995). Roots were separated by flotation method (McKell et al., 1961) and it was possible to distinguish the tree roots from these herbaceous plants because of differences in morphological aspects and the resistance to breaking of the woody roots (Böhm, 1979). Roots samples were dried out at 80°C until constant dry mass. The previous procedure indicated that four plots of 25 m^2 were needed for 20% precision in the belowground determinations.

2.3.2. Herbaceous components. Aboveground and belowground carbon stocks

At the protected plot, the herbaceous phytomass was determined when censuses for tree height were carried out at each age state. Ten samples, each 16 m^2, were harvested at random for peak aboveground phytomass. As the herbaceous layer composition changed along gradients extending from beneath trees to between trees, we just sampled between the trees for dealing with this spatial variation at the plot scale. At harvest time, the material was separated by species into assimilatory and non-assimilatory phytomass material. Samples were oven dried at 80°C to a constant dry mass.

At each aboveground sampling, three soil samples, each 4 m^2 were chosen to estimate belowground dry mass (Weigert, 1962). The samples were dug up to 0.3 m, where soil contains more than 80% of the total belowground dry mass (San Jose et al., 1985). Roots were separated by the flotation method (McKell et al., 1961) and oven dried at 80°C to a constant dry mass.

2.3.3. Calculation of areal carbon stock encompassing woody and herbaceous components

Areal carbon stock was obtained by summing area-weighted plots estimates from the area covered by woody and herbaceous within the protected plot. The woody vegetation area was calculated from the horizontal projection of the tree crowns by taking the elliptical axes. A temporal series of aerial photographs (1:25.000) corresponding to the censused data, were used to validate the calculated tree crown area. The carbon density in the dry mass of the vegetation was calculated using the proportion of carbon in woody and herbaceous vegetations (43%) as found by Hedges et al. (1986).

2.3.4. Soil component

At each age state, triplicates of soil samples were taken up to 1 m at 0.1 m depth increment for the percent of organic carbon by the Walkley and Black method (Jackson, 1958). The percent of soil organic matter was converted to percent of total organic carbon by dividing the percent of total organic matter by 1.724. The factor 1.724 is based on the assumption that carbon constitutes about 58% of the soil organic matter (Cox, 1972). Subsequently, the percent of total organic carbon was converted to g C m^2 by correcting the percent of total organic carbon for readily oxidizable carbon as it was by 0.77 (Walkley, 1947) and relating the corrected values to soil volume by considering soil bulk density. Soil bulk density was determined by the method proposed by Pla Sentis (1977).

3. Results

3.1. Allometric relationships

The relationship between total aboveground dry phytomass (Y) and plant height (x) were statistically fitted (Table 1) using the equations: (1) $Y = ae^{bx}$; (2) $Y = ab^{x}$; (3) $Y = ae^{b/x}$ and (4) $Y = ax^{b}$. Standard errors of the regression coefficients (Sokal and Rohlf, 1981) ranged from 0.015 to 0.355 for all tree species. Systematic error in the logarithmic calculations was corrected by following Baskerville (1972) and Beauchamp and Olson (1973).

Above 83% of the variance in dry mass was explained by tree height. The test for equality of slopes (Sokal and Rohlf, 1981) indicated that height–biomass relationships differed significantly among species. An exception of these results were the equation for *Bactris* sp. and *Casearia hirsuta*. Therefore, we used species-specific regressions for estimating biomass.

The accuracy of the assessments was evidenced when the regression estimates were compared with the harvesting of the aboveground dry mass from four savanna stands of 625 m^2 each, which included a density spanned from 300 to 1000 individuals ha^{-1}. This density range represents the change in density measured in the protected plot throughout time (San Jose and Fariñas, 1991). The calculated results based on allometric relationships were different, 12% in relation to the harvested aboveground dry mass.

3.2. Carbon stocks and fluxes with the conversion of savanna to a semi-deciduous forest

Temporal changes in the woody carbon stock from a protected savanna to a semi-deciduous forest

Table 1
Allometric relationships between dry mass in grams (Y) and plant height (x) (m) for the specie growing in the Biological Reserve of the Orinoco Llanos

Species	Model	Coefficient a	Coefficient b	S.E.
Allophylus occidentalis Radl.	1	419.90	0.64	0.125
Bactris sp.	3	18 704.71	7.13	0.290
Bowdichia virgilioides HBK	4	184.61	3.39	0.116
Byrsonima crassifolia HBK	4	342.92	3.21	0.089
Caesalpinia coriaria Willd	1	28.23	1.19	0.036
Casearia decandra Jacq.	4	106.81	3.07	0.176
Casearia hirsuta Sw.	3	19 651.43	−6.53	0.312
Cassia moschata HBK	4	186.63	3.12	0.176
Cecropia peltata L.	4	106.28	3.11	0.321
Cereus jamacaru DC.	1	281.22	0.59	0.061
Cochlospermum vitifolium (Willd.) Spreng	4	40.61	3.10	0.106
Connarus venezuelensis Baill	1	105.79	0.71	0.058
Copaifera officinalis HBK	4	9.84	4.10	0.338
Cordia hirta Johnston	4	85.84	2.69	0.159
Curatella americana L.	4	486.82	2.98	0.126
Fagara caribaea Engl.	1	264.91	0.61	0.042
Ficus sp.	1	257.75	0.55	0.045
Genipa caruto HBK	1	275.17	0.74	0.041
Godmania macrocarpa Hemsley	1	444.47	0.53	0.023
Guazuma ulmifolia Lam	4	15.65	3.80	0.213
Guettarda elliptica Sw	1	168.69	0.60	0.019
Lonchocarpus ernestii Harms.	4	25.14	3.47	0.118
Mimosa tenuiflora L.	4	198.60	2.51	0.079
Luehea candida (DC) Mart.	1	531.88	0.50	0.036
Machaerium pseudoacutifolium Pittier	1	208.68	0.62	0.052
Pithecellobium carabobense Harms	4	23.78	3.74	0.355
Platymiscium pinnatum (Jacq.) Dugan	1	166.00	0.065	0.057
Protium sp.	4	218.62	1.99	0.186
Pterocarpus podocarpus Blake	1	163.32	0.53	0.027
Spondias mombin L.	4	54.07	3.45	0.189
Tabebuia blakeana Pittier	1	254.70	0.64	0.053
Vitex appuni Moldenke	1	194.82	0.78	0.037
Vochysia venezuelana Stafleu	1	174.00	0.60	0.019
Xylopia aromatica (Lam.) Mart.	1	376.24	0.52	0.015
Xylosma pallidifolium Sleumer	4	241.93	2.55	0.190

Model number (1) $Y = ae^{bx}$; (2) $Y = ab^{x}$; (3) $Y = ae^{b/x}$ and (4) $Y = ax^{b}$.
a and b are the coefficients for the model and S.E. is the standard error of the regression coefficient (b)

are shown in Table 2. This forest represents the restored vegetational step following savanna protection (San Jose et al., 1991). Results (Table 2) indicate that after protection, the aboveground carbon stock in the woody vegetation increased from 20 g C m^{2} in the burned savanna to 8006 g C m^{-2} in the forest (390-fold). The belowground carbon stock increased from 15 to 1209 g C m^{-2} and the total carbon sequestration in the vegetation increased from 36 to 9215 g C m^{-2}.

Before protection, pyro-resistant species (Table 2) (*Curatella americana*, *Byrsonima crassifolia* and *Bowdichia virgilioides*) in the burned savanna accumulated 98% of the aboveground carbon stocks in the vegetation. After 25 years of protection, these species retained 50% of the aboveground carbon stock accumulated by the community. Among the non-resistant, the species *Cochlospermum vitifolium* accumulated the relatively greater percent of carbon (3%). In the forest, these pyro-resistant species stored

Table 2
Temporal changes in the plant carbon stock (C g m^{-2}) of all tree species in the censuses of a savanna plot (3 ha) protected against fire and cattle grazing since 1961 as compared to carbon stock in a semi-deciduous forest at the Orinoco Llanos. Woody cover was determined from aerial photographs

Species	Burned savanna	Years after savanna protection			Semi-deciduous forest
		8	16	25	
Allophylus occidentalis Radl.	–	–	–	4.329	–
Bactris sp.	–	–	0.016	0.034	0.459
Bowdichia virgilioides HBK	4.357	5.703	14.343	30.277	291.032
Byrsonima crassifolia HBK	14.583	23.553	26.802	157.804	566.774
Caesalpinia coriaria Willd	–	–	–	–	5.163
Casearia decandra Jacq.	–	0.074	0.885	12.082	2.698
Casearia hirsuta Sw.	–	–	–	2.071	–
Cassia moschata HBK	0.249	0.624	0.651	5.741	1225.810
Cecropia peltata L.	–	–	–	8.107	
Cereus jamacaru DC.	–	–	–	–	0.046
Cochlospermum vitifolium (Willd.) Spreng	–	0.110	1.419	15.113	375.042
Connarus venezuelensis Baill	–	0.001	0.006	0.089	0.028
Copaifera officinalis HBK	–	–	0.002	0.079	1448.045
Cordia hirta Johnston	–	0.066	0.017	1.098	0.857
Curatella americana L.	1.364	9.387	25.090	202.887	869.886
Fagara caribaea Engl.	–	–	0.002	0.360	61.813
Ficus sp.	–	–	–	–	662.182
Genipa caruto HBK	–	0.114	0.454	3.478	28.707
Godmania macrocarpa Hemsley	–	0.209	0.201	6.710	95.444
Guazuma ulmifolia Lam	–	–	–	–	41.581
Guettarda elliptica Sw	–	0.066	0.262	9.288	121.510
Lonchocarpus ernestii Harms.	–	–	–	–	194.135
Mimosa tenuiflora L.	–	–	–	0.003	–
Luehea candida (DC) Mart.	–	–	0.149	5.257	0.338
Machaerium pseudoacutifolium Pittier	–	–	0.063	1.958	341.544
Pithecellobium carabobense Harms	–	–	–	–	3.237
Platymiscium pinnatum (Jacq.) Dugan	–	0.008	0.037	1.162	121.781
Protium sp.	–	–	–	1.514	–
Pterocarpus podocarpus Blake	–	–	–	1.992	157.102
Spondias mombin L.	–	–	–	2.217	3.160
Tabebuia blakeana Pittier	–	–	–	0.575	14.719
Vitex appuni Moldenke	–	–	–	–	1311.027
Vochysia venezuelana Stafleu	–	–	0.016	0.068	53.703
Xylopia aromatica (Lam.) Mart.	–	–	0.069	0.405	–
Xylosma pallidifolium Sleumer	–	–	0.000	0.001	–
Aboveground carbon stock (g C m^{-2})	20.566	39.889	70.742	463.652	8006.000
Belowground carbon stock (g C m^{-2}) in vegetation	15.507	25.616	31.824	162.497	1209.300
Total	36.073	65.505	102.566	626.149	9215.300
Annual mean absolute C uptake rate (g C m^{-2} yr^{-1})	4.205	4.632	58.175		
Annual mean relative C uptake rate (g C m^{-2} yr^{-1})	0.085	0.056	0.201		

21% of the aboveground carbon stock. Only three species (*Copaifera officinalis*, *Vitex appuni* and *Cassia moschata*) accumulated 48% of the total aboveground carbon. These results indicate that after savanna protection, there were few species determining the carbon partitioning in the vegetation. As the protection time proceeded, species invaded the plot and total carbon in the community was stored by a larger number of species. In the forest, the species individually accumulated less than 20% of the aboveground carbon stock in the community.

The total carbon stock (W) as a function of the protection time (t) was expressed by the following equation: $W = 26.655\ e^{0.114\ t}$; $r^2 = 0.99$; Fs = 124.3. This equation was used to calculate the restoration time of the protected vegetation to reach a forest state. Consequently, it was estimated in 51 years.

The annual mean absolute carbon uptake rate (AMACUR) (Table 2) of the vegetation was calculated for each protection interval by using the data from the increment in carbon stock (ΔW) and its respective interval of time (Δt). This rate is given by the following equation (Watson, 1952; Lieth, 1965) $\mathrm{AMACUR} = \Delta W / \Delta t$. The calculated AMACUR varied from 4 to 58 C g m^{-2} yr^{-1}. The annual mean relative carbon uptake rate (AMACUR) was evaluated from the equation (Blackman, 1919; Fisher, 1921) $\mathrm{AMACUR} = (\ln W_2 - \ln W_1)/\Delta t$. The calculated annual mean absolute carbon uptake (AMACUR) of the vegetation varied throughout the protection time from 0.085 to 0.201 g m^{-2} yr^{-1}.

3.3. Areal carbon stock in the temporal scaling vegetation considering the weighted areas of the herbaceous and woody layers

In the burned savanna vegetation (Table 3), the areal aboveground carbon stock encompassing the weighted herbaceous and woody components was 228 g C m^{-2}. After protection, the areal aboveground stock increased to 8006 g C m^{-2} in the forest. The areal belowground carbon stock increased from 172 to 1209 g C m^{-2}. Thus, after protection, the areal total carbon stock in the vegetation increased from 407 to 9215 g C m^{-2}. Therefore, the forest stored 22-fold more carbon than that in the burned savanna. This increment of carbon density reflects a greater carbon stored in the aboveground compartment (35-fold) as compared to that in the belowground compartment (seven-fold). The areal

Table 3
Temporal changes in the plant carbon stock (g C m^{-2}) of the herbaceous, woody and soil components in the savanna and semi-deciduous forest groves of the Orinoco Llanos. Woody cover was determined from aerial photographs

	Burned savanna	Years after savanna protection			Semi-deciduous forest
		8	16	25	
Aboveground carbon stock					
Herbaceous component	207.937	279.223	453.270	322.199	–
Woody component	20.566	39.889	70.742	463.652	8006.0
Total	228.500	319.112	524.012	785.852	8006.0
Belowground carbon stock					
Herbaceous component	156.793	179.312	203.914	112.922	–
Woody component	15.507	25.616	31.824	162.497	1209.3
Total	172.300	204.929	235.739	275.419	1209.3
Total carbon stock					
Herbaceous component	364.730	458.535	657.184	435.121	–
Woody component	36.073	65.505	102.566	626.149	9215.3
Total vegetation carbon stock	400.806	524.040	759.750	1060.270	9215.3
Soil carbon stock					
Associated with herbs	5339.1	5166.7	5093.1	2414.0	–
Associated with trees	1341.5	1494.0	1646.4	7195.6	12 196.0
Total soil carbon stock	6680.6	6670.7	6639.5	9609.6	12 196.0
Total system carbon stock	7081.406	6941.100	7399.250	10 670.870	21 411.3

carbon stock in the soil of the burned savanna reached 75% of the total carbon stored in the system. Whereas in the forest, it was 56%.

In the herbaceous layer, the total sequestered carbon increased from 364 to 657 g C m^{-2} during 16 years of protection. Thereafter, it decreased up to 435 g C m^{-2}. Whereas, in the woody layer, it increased throughout the protection time from 36 to 626 g C m^{-2}. In the soil of the herbaceous layer, the carbon stock decreased from 5339 to 2414 g C m^{-2}. Whereas, in the woody layer, it increased from 1341 to 9609 g C m^{-2}. The forest stored three-fold more carbon (21 411 g C m^{-2}) in both the vegetation and soil compartments than that in the burned savanna (7081 g C m^{-2}).

4. Discussion

Results indicated that burned savannas of the Orinoco Llanos released from 97 g C m^{-2} yr^{-1}. This value was corrected for the production of charcoal during pyrolysis (18–24% for grasses on an ash-free dry mass basis) as well as for the emission of particulates from the savannas (1 g 100 g^{-1} of burned organic matter) (Seiler and Crutzen, 1980). If the surface covered by the Orinoco plains (0.28 × 1012 m^2) was behaving in the same way as these types of savanna and the average burning efficiency was 75% (Seiler and Crutzen, 1980), then the carbon released by burning savannas would be 0.020 Pg C yr^{-1}. A relatively lower value (0.0031 Pg C yr^{-1}) was estimated by the Venezuelan Environmental Ministry (MARNR, 1995) using an average burned efficiency of 13%. However, if the efficiency were 75%, such as that proposed by Seiler and Crutzen (1980), then the estimated carbon released using the data from MARNR (1995) would be 0.0178 Pg C yr^{-1}, which is similar to that reported here. Our value represent 0.7% of the annual carbon output from savanna burning around the world (2–4 Pg C yr^{-1}) as proposed by Seiler and Crutzen (1980). For the entire tropics, the net annual source from the Orinoco savannas represents 10% of the carbon released from humid savannas (0.12–0.30 Pg C yr^{-1}) as estimated by Lanly (1982) due to land use change.

In the protected savanna systems, change in carbon stock occurred with the invasion of woody species. It affected the relative proportion and production of the tree/grass components. Such changes result in modification of the carbon stocks in the herbaceous and woody components as well as in the soil. Thus, a protection consequence was to increase the total areal carbon stock from 7081 to 21 411 g C m^{-2}. This variation was mainly due to a carbon increase in the vegetation from 400 to 9215 g C m^{-2} (22-fold); whereas in the soil, it spanned from 6680 to 12 196 g C m^{-2}, (2-fold). The carbon increase in the vegetation reflects a major variation in the carbon stock of the woody layer from 36 to 9215 g C m^{-2} (255-fold). Therefore, after the protection, the woody layer was the major sink for carbon sequestering. A similar sequestered amount of carbon (4000 to 10 000 g C m^{-2}) has been reported for tropical open forest by Whittaker and Likens (1973), Seiler and Crutzen, 1980, Brown and Lugo (1984). Thus, tree invasion of the protected savanna represents a terrestrial sink, with an annual mean strength of 45 g C m^{-2} yr^{-1}.

In the burned savanna and forest, the soil carbon stock was 6680 and 12 196 g C m^{-2}, respectively. These values were lower as compared to those in the native savannas of Carimagua and Matazul Farm at the Meta plains, Colombia (18 650–19 700 g C m^{-2}) (Fisher et al., 1994). This variation might reflect unlikeness in species composition, soil types including depth of sampling and climatic conditions. If the differences between the soil carbon stock in the burned savanna and forest were used to estimate the carbon release from a disturbed forest soil, then the suggested annual carbon lost would be 108 g C m^{-2} yr^{-1}, which represent 45% of the total soil carbon in the forest. Similar maximum finding (114 g C m^{-2} yr^{-1}) has been reported by Seiler and Crutzen (1980). However, a literature review suggests a relatively lower reduction (20–25%) as a typical value for loss of carbon from soils after disturbance (Schlesinger, 1986; Detwiler et al., 1985).

The data from the changes in the areal carbon stock from the protected savannas toward a semi-deciduous forest could be used to infer the carbon sequestering pool by the forest vegetation in the Orinoco Llanos. Thus, if the total carbon stock in the analyzed forest was 21 411 g C m^{-2} and if the area covered by the Orinoco plains (0.28 × 10^{12} m^2 in area) in northern South America was behaving in the same way as this type of vegetation, then the sequestering pool of carbon in the restored forest would be 5.99 Pg C in 51 years. The assumption of a semi-deciduous forest covering partially the Orinoco Llanos is based on the studies of the permanent plot (San Jose et al., 1994) and the bio-climatic features of the Orinoco Llanos as a dry tropical forest as outline by the Holdrige's approach (Ewel and Madriz, 1968). In the vegetation of the semi-deciduous forest, the carbon pool (2.58 Pg C) represents 44% of the total carbon pool calculated for open forests of tropical America (Brown and Lugo, 1984). Therefore, a protected vegetation sink might remove CO_2 from the atmosphere to compensate for CO_2 emissions, and it might provide a means of controlling CO_2 concentration. As a result of protection of the savannas as well as expansion and conservation of the semi-deciduous forest in the Orinoco Llanos, significant quantities of carbon could be sequestered in the region. Natural regeneration of disturbed forest seems to have a larger effect on carbon sequestration as compared to plantation and agroforestry (Houghton, 1991a,b; Trexler and Haugen, 1993). Recently, evaluations of forests as carbon sources and sinks has been carried out at different latitudes (Wisniewski and Sampson, 1993; Dixon et al., 1994; Rodriguez Murillo, 1997).

The results of the present work indicate that savannas could accumulate carbon over decades if they were protected. Such changes would result not only in modification of the carbon stocks in the herbaceous and woody components, but also in feedback effects on atmospheric properties as related to variation in albedo and hydrological features (Reck, 1989), thereby affecting the water balance and local energy balance.

Year-to-year fluctuations in the carbon balance budget of the semi-deciduous forest of the Orinoco Llanos seems to be considerable. Thus, in a forest patch, the difference between soil respiration (Zelwer, 1969) and litter production might be up to 124 g C m^{-2} yr^{-1}. Such results demonstrate the potential of the forest to act as a carbon source. If all the forest of the Orinoco Basin (0.28×10^{12} m^2) were behaving in the same way as the semi-deciduous forest, the carbon source in the basin would be 0.034 Pg C yr^{-1}. On the other hands, the undisturbed tropical forest accumulated (0.56 Pg yr^{-1}) in southwest Amazonian (Grace et al., 1995). Therefore, year-to-year fluctuations in the carbon balance budget in mature forest would result in an annual carbon uptake or release from the system. Therefore, long term measurements will be necessary in order to obtain a net result of the system as carbon sink or source in the global carbon cycle. Furthermore, nutrients and water might constrain community CO_2 uptake, and as a consequence of climatic change, the carbon released by respiration and decomposition might increase (Ojima et al., 1993; Cebrian and Duarte, 1995; Parton et al., 1995). In the atmosphere, the equilibrium condition seems to be changing as the level of the atmospheric CO_2 increases up to 2 ppm yr^{-1} due to fossil fuel combustion and land use change (Detwiler et al., 1985; King et al., 1992). Therefore, net uptake of CO_2 by the mature forest communities can decrease the greenhouse effect (FAO, 1983; Lugo and Brown, 1992; Wofsy et al., 1993; Grace et al., 1995).

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