Carbon and nutrient accumulation in secondary forests regenerating from degraded pastures in central Amazônia, Brazil

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Abstract

Over the past three decades, large expanses of forest in the Amazon Basin were converted to pasture, many of which later degraded to woody fallows and were abandoned. While the majority of tropical secondary forest (SF) studies have examined post-deforestation or post-agricultural succession, we examined post-pasture forest recovery in ten forests ranging in age from 0 to 14 yrs since abandonment. We measured aboveground biomass and soil nutrients to 45 cm depth, and computed total site C and nutrient stocks to gain an understanding of the dynamics of nutrient and C buildup in regenerating SF in central Amazônia. Aboveground biomass accrual was rapid, 11.0 Mg ha^{-1} yr^{-1}, in these young SF. After 12 to 14 yrs, they accumulated up to 128.1 Mg/ha of dry aboveground biomass, equivalent to 25 to 50% of primary forest biomass in the region. Wood N and P concentrations decreased with forest age. Aboveground P and Ca stocks accumulated at a rate of 2.4 and 42.9 kg ha^{-1} yr^{-1}; extractable soil P stocks declined as forest age increased. Although soil stocks of exchangeable Ca (207.0 ± 23.7 kg/ha) and extractable P (8.3 ± 1.5 kg/ha) were low in the first 45 cm, both were rapidly translocated from soil to plant pools. Soil N stocks increased with forest age (117.8 kg ha^{-1} yr^{-1}), probably due to N fixation, atmospheric deposition, and/or subsoil mining. Total soil C storage to 45 cm depth ranged between 42 and 84 Mg/ha, with the first 15 cm storing 40 to 45% of the total. Total C accrual (7.04 Mg C ha^{-1} yr^{-1}) in both aboveground and soil pools was similar or higher than values reported in other studies. Tropical SF regrowing on lightly to moderately-used pasture rapidly sequester C and rebuild total nutrient capital following pasture abandonment. Translocation of some nutrients from deep soil (>45 cm depth) may be important to sustaining productivity and continuing biomass accumulation in these forests. The soil pool represents the greatest potential for long-term C gains; however, soil nutrient deficits may limit future productivity.

Keywords: secondary forest; abandoned pasture; carbon sequestration; plant nutrient stocks; soil nutrient stocks; nutrient loss; Oxisol; succession; Amazon.

Introduction

Primary forest conversion for subsistence agriculture, industrial logging and pasture establishment continues to be the predominant cause of tropical deforestation (Laurance, 1999). These activities have left a large portion of the tropical biome disturbed and in various states of natural regeneration (Brown and Lugo, 1990), stagnation (Fearnside and Guimaraes, 1996; Sarmiento, 1997; Silver et al., 2000), or managed recovery (Fernandes and Matos, 1995; Parrotta et al., 1997). Of the estimated 58.8 million ha of forest cleared in Brazilian Amazônia over the past three decades (INPE, 2002), approximately 24 million ha were converted to pastures (Serrão et al., 1995). Depending on management (replacement of exported or lost nutrients, stocking rates, burning frequency, etc.), region, and soil type, pasture productivity may

decline after 7 to 10 years and may be recleared or abandoned to recolonizing secondary vegetation; approximately 50% of the first-cycle pastures have reached this advanced stage of degradation (Serrao et al., 1993). Based on an analysis of 1990 land use data in the Amazon, Fearnside (1996) calculated an equilibrium will be reached where ~47% of all deforested land would be regenerating forest on degraded or abandoned pastures.

Although highly altered, these lands are valuable for human use (Brown and Lugo, 1990), and provide important ecosystem services such as watershed protection, sources and havens of biodiversity, erosion prevention, soil fertility recovery by improved fallows (Szott et al., 1991), and atmospheric C sinks (Fearnside and Guimaraes, 1996, Silver et al., 2000). However, the potential of the abandoned land to recover and maintain these roles is dependant on the intensity of previous land use (Uhl et al., 1988; Nepstad et al., 1990; Aide et al., 1995; Alves et al., 1997), soil nutrient limitations (Cochrane and Sánchez, 1982; Smyth and Cravo, 1992; Laurance et al., 1999), and seed inputs and seedling establishment (Nepstad et al., 1996). These impediments to vegetation regrowth may be more extreme in abandoned pastures compared to agricultural land, resulting in lower aboveground productivity (Fearnside and Guimaraes, 1996; Silver et al., 2000), and longer regeneration times.

Pasture productivity declines rapidly with decreasing soil P availability, facilitating invasion by secondary forest (SF) species better adapted to infertile soil (Toledo and Navas, 1986); yet, soil fertility and biomass recovery is variable and dependant upon several factors. Degraded pastures are characterized by depleted soil nutrient stocks, low vegetation biomass, low primary forest seed inputs, high seed predation, depleted seed bank of forest species and low stump sprouting (Nepstad et al., 1990), as well as soil surface sealing and compaction (Eden et al., 1991). Consequently, predicting the long-term growth rate of secondary vegetation on degraded pastures and the return of primary forest characteristics becomes a complex task.

New attention has focused on fast-growing SF due to their potential to sequester large quantities of C in short time-periods. For example, worldwide tropical forests store approximately 206 Pg C in the soil (Eswaran et al., 1993), and tropical SF of less than 20 years have the potential to accrue soil C at a rate of 1.3 Mg ha^{-1} yr^{-1} (Silver et al. 2000). The growth rate of young SF is expected to increase with rising atmospheric CO_2 levels (DeLucia et al., 1999); however, high C allocation to short-lived tissues such as leaves and faster turnover of litter C may limit the potential C sink (Schlesinger and Lichter, 2001). Furthermore, soil nutrient limitations may constrain primary productivity under CO_2 enrichment (Oren et al., 2001).

Soil nutrient impediments to productivity under native vegetation are substantial in the Brazilian Amazon. Cochrane and Sánchez (1982) estimated that only 7% of the land area is free from major plant growth limitations; soil P deficiencies (<7 mg/kg) constrain productivity in 90% (436 million ha), and Al toxicity (Al saturation of $\geq$ 60%) occurs over 73% of the Brazilian Amazon. Low soil Ca (Smyth and Cravo, 1992) restrains productivity, P deficiencies (Gehring et al., 1999) limit SF growth, and the vegetation is unable to effectively capture leaching soil N (Schroth et al., 1999). Mismanagement may compound these deficiencies since pasture use-intensity appears to negatively influence regenerating vegetation biomass (Uhl et al., 1988) and nutrient stocks (Buschbacher et al., 1988). Because SF recovery is variable and dependent on previous land-use and soil fertility, the magnitude and rate of the above- and below-ground C accumulation in these regenerating SF is still relatively unknown.

Determining nutrient constraints to regrowth and the status of secondary vegetation is an important step in managing and/or enhancing abandoned site rehabilitation. We examined the dual roles of SF to rehabilitate site productivity and to increase C sinks and investigated potential soil nutrient limitations to these two processes. We examined aboveground and soil C accrual and nutrient stocks in degraded pastures that had been abandoned for a varying number of years. Our objective was to study the influence of regenerating vegetation on C and nutrient budgets following pasture abandonment. We hypothesized that C and N pools would recover with time following post-burn volatilization, while other nutrients would be redistributed from below- to above-ground pools resulting in reduced soil pools.

Methods

Study area

The study areas are located in Amazonas, Brazil, in the central Amazon Basin, north of the city of Manaus along the road BR-174. The study area spans approximately 26 km (2° 34' S, 60° 02' W and 2° 20' S, 60° 04' W). The terrain is undulating with an elevation of 50-150 m. The plateau soil is classified as dystrophic, isohyperthermic, clayey kaolinitic, Hapludox with approximately 80–85% clay (*latossolo amarelo* according to the Brazilian classification system). Slope soils are composed of Ultisols and valley bottoms by Spodosols. The plateau soils have a low cation exchange capacity and are infertile but are strongly aggregated and well drained (Van Wambeke,1992).

The regional climate is tropical humid and the mean temperature is 26.7°C. Mean annual rainfall in Manaus is 2.2 m, with March and April as the wettest months with over 300 mm of precipitation. A mild dry season occurs from August through October, with mean monthly precipitation falling below 100 mm, and in some El Niño years to as little as 50 mm (Lovejoy and Bierregaard, 1990).

The native vegetation of this region is closed-canopy, dense, evergreen *terra firme* forest (Veloso et al., 1991). Species recovery with SF development is significantly different in areas used as pasture compared to areas cut but not managed (Mesquita et al., 2001). Old growth, native vegetation remains the dominant cover in this area. The establishment of new pastures is now rare, and active pastures are a diminishing, short-lived feature of the landscape north of Manaus. However, SF are increasingly found along the primary roads where efforts to raise cattle on large ranches failed some 10 to 20 years ago.

A majority of the pastures were mechanically cleared in the early 1980's, commercial timber may or may not have been removed, the slash burned in place or mechanically piled in windrows, and the area planted with exotic African grasses such as *Brachiaria brizantha* or *B. humidicola* (Rendle). Standard pasture management for the region includes at least one application of 50 kg P/ha. The animal stocking rate and number of years that the pastures were grazed were variable. Overgrazing and annual burning to increase economic returns in the short-term accelerated pasture degradation through increased nutrient loss and soil compaction. However, even in the absence of overgrazing (1–2 animal/ha) increases in bulk density occur (0.4 g/cm^3 increase from forest values after 12 years as pasture), leading to reduced infiltration, sheetwash, and pasture decline (Eden et al., 1991). Declining pasture productivity is characterized by a reduction in the forage to weed ratio as bare ground develops and herbaceous and woody plants begin to invade. When unpalatable plants begin to dominate, livestock productivity drops, animal mortality increases and the pasture is eventually abandoned. Fire and/or labor intensive hand weeding of seedlings and roots may lengthen pasture life by reducing woody biomass while encouraging grass growth; however, species of *Vismia*, a fast-growing early successional tree, resprout rapidly after burning and dominate abandoned pastures.

Site and plot selection

Ten SF were selected within three *fazendas* (cattle ranches) now in various stages of grazing, pasture abandonment or pasture reclamation: Fazenda Rodão (km 46), the Brazilian Agency for Agricultural Research (Embrapa Amazônia Ocidental) Agricultural District of SUFRAMA (DAS) pasture research site (km 53), and Fazenda Dimona (km 72), all along the road BR–174. Within each forest located on plateau Oxisols, we established four plots of 100 m^2 to 400 m^2, each with three subplots ranging in size from 35 to 225 m^2 depending on forest age. Forests ranged from 0 to 2 yrs to 12 to 14 yrs since pasture abandonment. Secondary forest selection was based on forest age and independence from adjacent plots within the same ranch. We selected a range of forests spanning the age of available SF in the area; however, all SF age classes do not occur at all farms. We conducted farmer interviews to determine site histories and when grazing was abandoned. The date at which the pastures were abandoned is not definitive, as cattle may infrequently graze the area until all palatable forage is replaced by woody successional vegetation. The regenerating forests within the ranches are biologically and physically distinct, each with a unique management history and vegetation cover.

Biomass and tissue analysis

Within each subplot, we measured diameter at breast height (DBH at 1.3 m above ground level; *Cecropia* were measured above prop-roots) for all live tree stems ≥1cm, tagged the stems, and recorded all species. Using two sets of allometric equations, Nelson et al. (1999) for stem >5 cm DBH and Mesquita (in preparation) for those 1 to 5 cm DBH, we calculated dry biomass for each tree and converted the estimates to Mg/ha. The two sets of equations were developed either on the EMBRAPA research site (Nelson et al., 1999) or within the same region (Mesquita, pers. comm). They provide a better estimate of SF biomass than previous equations (Saldarriaga et al., 1988; Uhl et al., 1988; Brown et al., 1989; Overman et al., 1994) developed in the Amazon Basin (Nelson et al., 1999). The Nelson equations provide valid biomass estimates from 1 to 30 cm DBH. However, since these SF have more stems in the smaller diameter range of the Mesquita equations (1 to 5 cm DBH), by using the two sets of equations rather than one, we improve biomass estimates.

We used species-specific equations for the dominant tree species *Vismia cayennensis* (Jacq.) Pers., *V. japurensis* Reich. (Clusiaceae); *Cecropia* (Moraceae; mainly *C. sciadophylla* Mart. and *C. purpurascens* C.C. Berg); *Bellucia* (Melastomataceae); *Goupia glabra* Aubl. (Celastraceae); *Laetia procera* (Poepp) Eichl. (Flacourtiaceae), and a mixed-species equation for all others. The pioneer *Cecropia*, uncommon on these sites, occurs less frequently in areas where grazing continues during secondary vegetation establishment (Mesquita et al. 2001).

To produce an aboveground forest estimate of nutrient concentrations (and nutrient stocks on a per hectare basis) within each forest, we randomly selected 15 trees ≥1 cm DBH and collected mature, upper canopy sun leaves using a telescoping tree pruner or climbing the boles. From the same trees, we drew two wood core samples (wood and bark) at 1.3 m height on opposite sides of the bole. Foliage and wood samples were pooled into three sample composites of five trees, oven dried at 70ºC, ground and homogenized, and analyzed for C, N, P, K, Ca, and Mg using standard EMBRAPA laboratory operating procedures (Silva, 1999).

Vegetation stocks calculations

We developed a foliage:wood ratio (Mesquita, in prep.) for partitioning biomass into wood and foliar components. We then estimated aboveground carbon and nutrient stocks in each forest by multiplying mean nutrient concentrations for foliage and wood samples by the allometric estimates of each biomass component as partitioned by the foliage to wood ratio for individual trees. Our estimates of nutrient pools do not include aboveground biomass <1cm DBH, forest litter, or root biomass.

Soil analysis

We sampled soil to 45 cm in three depth classes (0–15, 15–30, 30–45 cm) within each of four plots per forest. The four soil samples per depth in each forest (120 soil samples) represent a composite of four to six sub-samples per sample. Soil composites were combined in the field, air dried in solar dryers, charcoal and roots removed, hand milled with a roller, sieved to 2 mm, and analyzed for C, N, P, K, Ca, and Mg. Charcoal is common in local surface soils and is present at times to 45 cm depths in both pasture and forest soils. As charcoal is heterogeneously distributed in the soil, charcoal contamination poses an important impediment to resolution in reporting soil C concentrations. We estimate that carbon concentrations in this study, as with other studies within the Amazon basin, may generally overestimate total soil carbon stocks as a result of charcoal contamination (M.A. Rondón, unpublished data). To reduce the charcoal contribution to soil C estimates, large pieces were removed while the samples were wet and again with a forceps after drying before grinding; however, the small fragment size makes total removal difficult.

Extractable soil P and K were analyzed using a double acid extraction (0.05 M hydrochloric acid and 0.0125 M sulfuric acid) and exchangeable Ca and Mg with 1 M potassium chloride. Total soil N was determined by the Kjeldahl technique and soil C (%) by wet digestion (Silva, 1999). Soil nutrient pools (kg/ha) of C, N, P, K, Mg, and Ca were calculated using mean soil bulk density data measured to 45 cm depth from abandoned pastures and SF in the same area (T.R. Feldpausch; S.A. Welch, unpublished data).

Nutrient concentrations were multiplied by bulk densities for each depth class to provide soil nutrient stocks on a per hectare basis.

Statistical analysis

Statistical analyses were performed using Minitab 12.1 (Minitab Inc.). Statistical comparisons for C and nutrient concentrations and stocks were conducted separately for the different vegetation tissue types and soil depths using linear and log-linear regression and a $p<0.05$ significance level. Soil and vegetation concentrations, and soil stocks values were log transformed. Pooling the data for age classes and using regression analysis, we tested for trends in C and nutrients within aboveground and soil pools, as partitioned by depth, foliage or wood, versus time (years after pasture abandonment).

Results

A total of 1901 stems were measured in 2320 m^2, of which 138 standing dead and 177 lianas were excluded from biomass calculations due to allometric equation limitations in computing such components. Of those stems considered in biomass estimations, 68% were less than 5 cm DBH, while no stems were greater than 30 cm DBH. The two recently abandoned pastures of 0–2 years had no stems ≥1cm DBH, the minimum diameter used for the allometric equations.

Vegetation nutrient concentrations

Wood N and P concentrations declined with SF age (r^2 = 0.85, 0.75; $p<0.001$), with an average reduction of 50 and 60% in wood N and P from the youngest to the oldest forests. Foliage N and P concentrations tended to decline with forest age, although non-significantly. Compared to wood, foliage contained an average of 5.7 times more N and 3.7 times more P (Table 1).

Foliar and wood Ca concentrations did not show a trend with age, but the concentrations were high relative to other nutrients. Calcium concentrations in wood were comparable and at times higher than wood N values. n the foliage, Ca concentrations represented an average of 43% of N values. Foliage contained an average of 2.5 times more Ca than wood. Potassium and Mg foliar and wood concentrations showed no trends with forest age.

Vegetation nutrient stocks

Although woody biomass accumulated more quickly than foliage, nutrient stocks for all nutrients accumulated more quickly in foliage (Figure 1). Foliar N stocks (42.6 kg ha^{-1} yr^{-1}; r^2=0.94; $p<0.001$) increased much more rapidly than woody stocks (15.5 kg ha^{-1} yr^{-1}; r^2=0.91; $p<0.01$) with time after abandonment. Phosphorus stocks in foliage accrued twice as fast as wood P stocks. However, foliar Ca stocks (22.3 kg ha^{-1} yr^{-1}; r^2=0.92; $p<0.001$) accrued at a similar rate to wood stocks (20.6 kg ha^{-1} yr^{-1}; r^2=0.90; $p<0.001$) (Table 2).

Soil nutrient concentrations

Within each forest, soil carbon and nutrient concentrations generally decreased with depth (Table 3). Total soil N concentrations generally decreased with depth; however, deeper soil profile (30–45 cm depth) N concentrations increased with time after pasture abandonment (r^2 = 0.57; $p<0.001$), while the shallower depths showed a weaker soil N trend with time. Soil extractable P concentrations tended to decrease at all soil depths over time, with significant reductions in surface layers (0-15 cm depth) with increasing time since abandonment (r^2 = 0.46; $p<0.05$). Near surface Ca levels (0–15 cm depth) ranged from 0.13 to 0.33 c.mol$_{(+)}$/kg. Calcium concentrations were low below 15 cm depth, with overall means of 0.07 c.mol$_{(+)}$/kg at 15–30 cm and 0.07 c.mol$_{(+)}$/kg at 30–45 cm depths.

Table 1: Mean C and nutrient concentrations in foliage and wood from ten secondary forests regenerating from degraded pasture in central Amazônia, Brazil[a].

SF age (yrs)	Fazenda and forest no.	C	N	P	K	Ca	Mg
		%	--g / kg--				
Foliage							
0 to 2	DAS-1 and Rodão-1	46.65 (1.80)	17.11 (0.78)	0.87 (0.04)	3.71 (0.35)	7.25 (0.74)	2.31 (0.06)
2 to 4	Rodão-4	45.51 (0.33)	16.42 (0.06)	0.65 (0.03)	2.75 (0.00)	6.42 (0.17)	1.88 (0.02)
4 to 6	DAS-2 and Rodão-3	48.25 (1.26)	16.08 (0.82)	0.89 (0.04)	5.59 (1.16)	5.28 (0.14)	2.04 (0.28)
6 to 8	Dimona-1, -3 and Rodão-2	45.69 (0.59)	14.60 (0.50)	0.56 (0.03)	5.38 (0.71)	6.59 (0.41)	2.13 (0.19)
12 to 14	DAS-3 and Dimona-2	49.38 (0.64)	15.02 (0.16)	0.58 (0.02)	5.14 (0.29)	7.86 (0.12)	2.77 (0.12)
Overall Mean		47.12 (0.54)	15.66 (0.31)	0.70 (0.03)	4.78 (0.36)	6.70 (0.24)	2.25 (0.10)
Wood							
0 to 2	DAS-1 and Rodão-1	51.40 (0.49)	3.71 (0.31)	0.31 (0.01)	2.23 (0.33)	4.05 (0.58)	0.98 (0.11)
2 to 4	Rodão-4	47.64 (0.41)	2.99 (0.39)	0.19 (0.01)	1.19 (0.10)	2.76 (0.29)	0.69 (0.05)
4 to 6	DAS-2 and Rodão-3	47.45 (1.16)	2.80 (0.15)	0.21 (0.03)	1.69 (0.31)	2.01 (0.21)	0.47 (0.04)
6 to 8	Dimona-1, -3 and Rodão-2	47.68 (1.05)	2.52 (0.14)	0.16 (0.01)	1.76 (0.17)	2.33 (0.19)	0.55 (0.06)
12 to 14	DAS-3 and Dimona-2	51.05 (1.99)	1.87 (0.12)	0.09 (0.02)	1.28 (0.11)	2.51 (0.30)	0.58 (0.07)
Overall Mean		49.05 (0.63)	2.73 (0.14)	0.19 (0.01)	1.68 (0.12)	2.69 (0.19)	0.64 (0.04)

[a]Each mean nutrient concentration value represents n=3 samples of a five tree composite in each forest. Mean (standard error).

Table 2: Rate of total nutrient accumulation, vegetation nutrient immobilization (a), and soil nutrient flux to 45 cm depth (b). Results from ten secondary forests regenerating from degraded pastures in central Amazônia, Brazil.

	N	P	K	Ca	Mg
	--- kg ha^{-1} yr^{-1} ---				
Total vegetation and soil (a + b)[a]:	175.9 (r^2=0.62; p<0.001)	1.8 (r^2=0.75; p<0.01)	24.7 (r^2=0.88; p<0.001)	42.2 (r^2=0.84; p<0.001)	12.9 (r^2=0.79; p<0.001)
a. Total foliage and wood	58.1 (r^2=0.94; p<0.001)	2.4 (r^2=0.93; p<0.001)	25.1 (r^2=0.92; p<0.001)	42.9 (r^2=0.92; p<0.001)	12.5 (r^2=0.92; p<0.001)
Foliage	42.6 (r^2=0.94; p<0.001)	1.6 (r^2=0.95; p<0.001)	14.5 (r^2=0.90; p<0.001)	22.3 (r^2=0.92; p<0.001)	7.8 (r^2=0.90; p<0.001)
Wood	15.5 (r^2=0.91; p<0.001)	0.8 (r^2=0.72; p<-.01)	10.6 (r^2=0.89; p<0.001)	20.6 (r^2=0.90; p<0.001)	4.7 (r^2=0.93; p=<0.001)
b. Total soil[b]:	117.8 (r^2=0.44; p=0.04)	- 0.66 (r^2=0.34; p=0.08)	~ 0 (N.S.)	~ 0 (N.S.)	~ 0 (N.S.)

[a] Represents a new linear regression with the sum of the subtotals.
[b] Total nitrogen and extractable P, K, Ca, and Mg. N.S. indicates a non-significant change.

Table 3: Mean soil carbon and nutrient concentrations, and pH from ten secondary forests regenerating from degraded pasture in central Amazônia, Brazil[a].

SF age (yrs)	Fazenda and forest no.	C	N	P	K	Ca	Mg	Ph
		---- (g / kg) ----		---- (mg / kg) ----		---- (cmol$_{(+)}$ / kg) ----		(KCl)
0–15 cm depth								
0 to 2	DAS-1 and Rodão-1	15.39 (2.27)	1.23 (0.13)	4.83 (0.57)	20.98 (2.40)	0.13 (0.02)	0.09 (0.01)	4.1 (0.03)
2 to 4	Rodão-4	20.77 (2.64)	1.25 (0.09)	3.09 (0.17)	18.11 (0.82)	0.18 (0.01)	0.07 (<0.01)	4.0 (0.02)
4 to 6	DAS-2 and Rodão-3	20.71 (2.01)	1.42 (0.16)	6.30 (0.86)	33.20 (4.76)	0.16 (0.04)	0.14 (0.02)	4.0 (0.03)
6 to 8	Dimona-1, -3 and Rodão-2	22.91 (0.85)	1.49 (0.05)	2.46 (0.30)	23.92 (2.49)	0.33 (0.11)	0.18 (0.04)	4.0 (0.03)
12 to 14	DAS-3 and Dimona-2	19.51 (2.77)	1.75 (0.04)	1.55 (0.17)	19.45 (0.55)	0.16 (0.05)	0.11 (<0.01)	4.0 (0.01)
Overall mean		20.19 (0.94)	1.46 (0.05)	3.55 (0.36)	23.78 (1.52)	0.21 (0.04)	0.13 (0.02)	4.0 (0.01)
1 –30 cm depth								
0 to 2	DAS-1 and Rodão-1	9.17 (1.43)	0.74 (0.06)	2.03 (0.53)	8.46 (0.71)	0.08 (0.01)	0.05 (<0.01)	4.2 (0.02)
2 to 4	Rodão-4	17.14 (0.70)	0.91 (0.06)	1.87 (0.17)	10.53 (0.47)	0.11 (0.01)	0.05 (0.01)	4.2 (0.02)
4 to 6	DAS-2 and Rodão-3	10.63 (1.08)	0.86 (0.08)	1.40 (0.13)	10.86 (1.63)	0.08 (0.01)	0.05 (0.01)	4.1 (0.02)
6 to 8	Dimona-1, -3 and Rodão-2	12.09 (0.55)	0.88 (0.02)	0.86 (0.13)	11.19 (0.88)	0.05 (0.01)	0.04 (0.01)	4.1 (0.02)
12 to 14	DAS-3 and Dimona-2	11.46 (0.76)	1.01 (0.01)	0.70 (0.00)	8.56 (0.31)	0.07 (0.02)	0.05 (<0.01)	4.1 (0.02)
Overall mean		11.65 (0.52)	0.88 (0.03)	1.25 (0.13)	10.02 (0.48)	0.07 (0.01)	0.05 (<0.01)	4.1 (0.01)
30–45 cm depth								
0 to 2	DAS-1 and Rodão-1	6.57 (0.57)	0.55 (0.02)	1.15 (0.41)	5.56 (0.28)	0.06 (0.01)	0.04 (0.01)	4.2 (0.02)
2 to 4	Rodão-4	12.25 (0.86)	0.65 (0.07)	1.15 (0.16)	7.14 (0.46)	0.10 (0.02)	0.04 (<0.01)	4.2 (0.02)
4 to 6	DAS-2 and Rodão-3	10.84 (2.36)	0.65 (0.02)	0.86 (0.09)	5.84 (0.97)	0.07 (0.01)	0.04 (<0.01)	4.2 (0.02)
6 to 8	Dimona-1, -3 and Rodão-2	8.12 (0.66)	0.69 (0.01)	0.39 (0.10)	6.28 (0.58)	0.05 (0.01)	0.04 (0.01)	4.1 (0.02)
12 to 14	DAS-3 and Dimona-2	16.08 (2.49)	0.77 (0.02)	0.58 (0.09)	5.84 (0.39)	0.05 (0.01)	0.04 (<0.01)	4.1 (0.01)
Overall mean		10.46 (0.89)	0.67 (0.01)	0.74 (0.09)	6.06 (0.28)	0.06 (0.01)	0.04 (<0.01)	4.2 (0.01)

[a] Mean values are n=4 per depth in each forest from a composite of four to six sub-samples per sample and summarized by age class. Total carbon and nitrogen, extractable P and K, and exchangeable, Ca, and Mg. Mean (standard error).
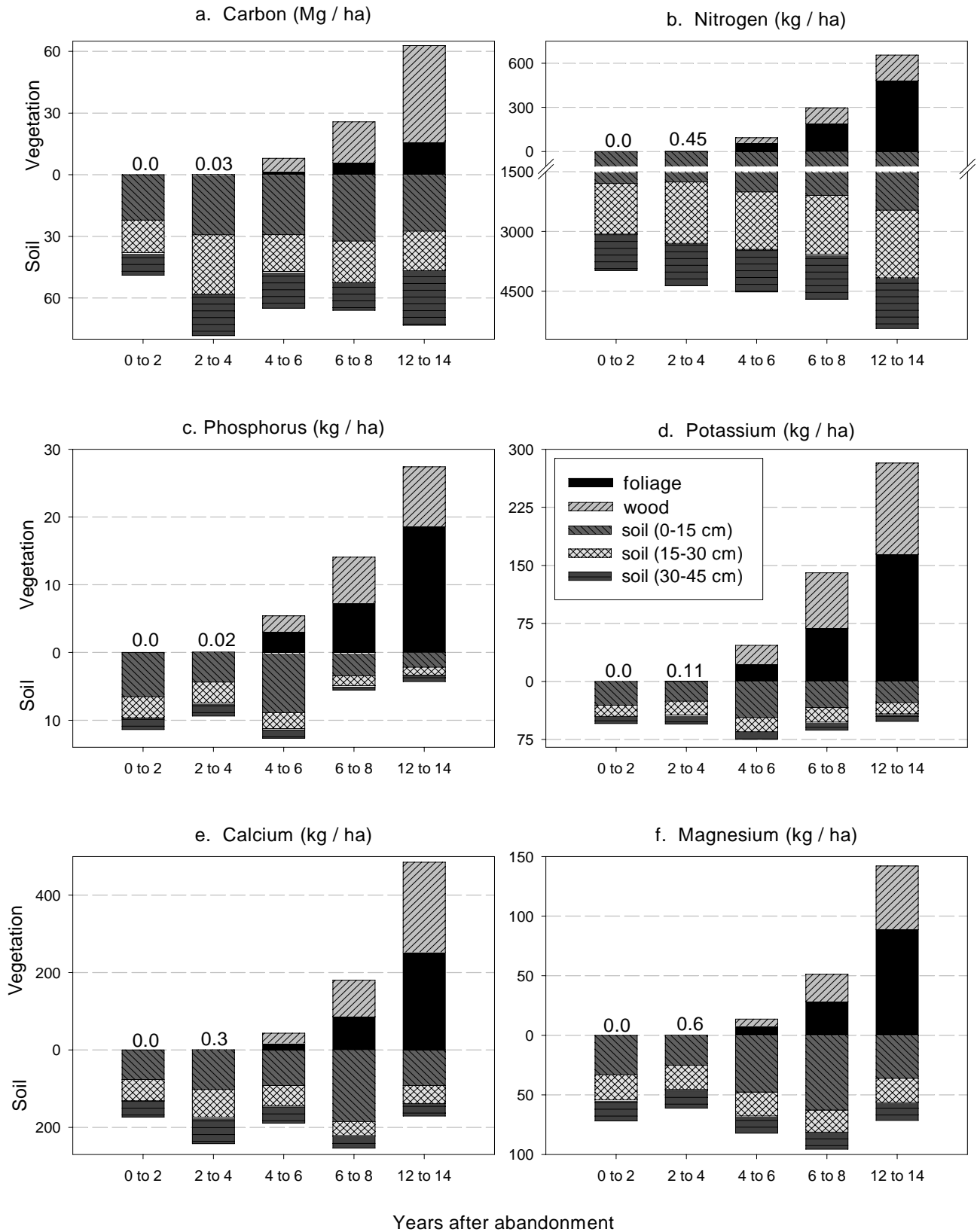
a. Carbon (Mg / ha)

b. Nitrogen (kg / ha)

c. Phosphorus (kg / ha)

d. Potassium (kg / ha)

Legend:
- foliage
- wood
- soil (0-15 cm)
- soil (15-30 cm)
- soil (30-45 cm)

e. Calcium (kg / ha)

f. Magnesium (kg / ha)

Years after abandonment

Figure 1 a – f: Total C, N, extractable P and K and exchangeable Ca and Mg in soils to 45 cm depth and live aboveground vegetation ≥1 cm DBH in ten secondary forests regenerating from degraded pastures in central Amazônia, Brazil. Mean nutrient stocks for each forest (see Table 1 for forest grouping by age-class) calculated from soil and vegetation nutrient concentrations times soil bulk density or aboveground biomass. Note the scale difference between N soil and aboveground stocks. Values above time 0 – 2 and 2 – 4 indicate aboveground quantities only.

Soil nutrient stocks

Soil extractable nutrient stocks were generally lower in deeper soil pools. Within the oldest forests, soil C, N, and Mg nutrient stocks were greater than aboveground nutrient stocks while the other nutrients resided predominantly within forest vegetation (Figure 1).

Soil N stocks, relative to aboveground stocks, were high, and increased with forest age at a rate of 117.8 kg ha^{-1} yr^{-1} ($r^2 = 0.44$; $p<0.05$). Pastures abandoned for twelve or more years stored 1.5 Mg/ha more total N to 45 cm depth than areas abandoned for two or fewer years (5.4 and 3.9 Mg N/ha). In all forests, surface nitrogen stocks (0–15 cm) represented approximately 40 to 45% of the total soil nitrogen to 45 cm depth (total 45 cm range: 3.3 to 5.5 Mg N/ha) (Figure 1).

Extractable soil P stocks to 45 cm tended to decline with increasing forest age (-0.66 kg ha^{-1} yr^{-1}), a trend most pronounced within the upper 0–15 cm. This surface layer represented 46 to 70% of total soil P stocks to 45 cm depth, with the younger areas, on average, storing 4.2 kg/ha more P in the first 15 cm than the oldest areas. Considering the entire measured soil profile (0–45 cm depth) higher extractable soil P stocks were observed in stands of 0 to 6 years (11.5 ± 4.6 kg/ha) compared to stands of 6–14 years (5.1 ± 2.1 kg/ha). Soil P in the 0–15 cm class was more variable than in deeper layers. Potassium, Ca, and Mg stocks remained constant with time after abandonment (Table 2).

Total nutrient stocks

There was a significant net gain in combined vegetation and soil nutrient stocks for all nutrients (Table 2). The total system P accumulation rate was slow and reflective of the counteracting decrease in soil P stocks with increasing forest age. Total system N stocks increased most rapidly followed by Ca. While total (biomass plus soil) nutrient stocks for all nutrients increased over time, in soils, only N increased significantly.

Carbon sequestration

Standing biomass. Foliar dry biomass in the ten forests grouped according to age after pasture abandonment (0–2, 2–4, 4–6, 6–8, 12–14 years) was 0.0, 0.02, 3.47, 13.10, 32.15 Mg/ha (Figure 1). Average biomass accrual for all SF through the first 12–14 years after pasture abandonment was 11.0 Mg ha^{-1} yr^{-1} (r^2=0.95, $p<0.001$), or 5.6 Mg C ha^{-1} yr^{-1} (r^2=0.94, $p<0.001$). As expected, carbon stocks in wood (4.2 Mg C ha^{-1} yr^{-1}) accrued more quickly than foliage C (1.4 Mg C ha^{-1} yr^{-1}) as forests matured (Table 4).

Table 4: Relationship between years after pasture abandonment (X) and the accumulation of aboveground biomass and carbon, and soil carbon (Mg ha^{-1} yr^{-1}) in ten secondary forests regenerating from degraded pastures in central Amazônia, Brazil.

Dependent Variable	Equation	(r^2)	(p)
Biomass[a]			
Foliage	Y = 2.85 X – 6.61	0.94	< 0.001
Wood	Y = 8.18 X – 17.32	0.95	< 0.001
Total foliage and wood	Y = 11.0 X – 23.92	0.95	< 0.001
Carbon			
Foliage[a]	Y = 1.40 X – 3.36	0.94	< 0.001
Wood[a]	Y = 4.15 X – 9.18	0.94	< 0.001
Total foliage and wood[a]	Y = 5.55 X – 12.54	0.94	< 0.001
Total soil[b]	Y = 1.49 X + 5.59	0.20	= 0.20
Total foliage, wood, and soil	Y = 7.04 X + 43.31	0.85	< 0.001

[a] All live trees ≥1 cm DBH with biomass converted to C based on site-specific foliage and wood C concentrations.
[b] Total soil C to 45 cm depth.

The greatest total biomass (128.1 Mg/ha) was measured in a SF with 12–14 years since abandonment; the areas abandoned 6–8 years had an average biomass of 54.4 Mg/ha, while the areas abandoned 4–6 years an average of 16.4 Mg/ha (Figure 1). Woody biomass in the ten SF by years after pasture abandonment was 0.0, 0.05, 12.92, 41.25, 92.24 Mg/ha in the 0–2, 2–4, 4–6, 6–8, and 12–14 year-old forests.

Soil Carbon. Soil carbon storage (excluding roots) tended to increase with forest age, with the oldest forests storing an average of 25 Mg/ha (65%) more total soil C to 45 cm depth than the youngest forests. Surface layers (0–15 cm) stored significantly more C (28.4 ± 2.4 Mg/ha) than deeper layers (18.3 ± 1.5 Mg/ha), from 24 to 50% of the total soil carbon to 45 cm depth in all forests ($p<0.001$). However, the oldest forests, 12–14 yr-old, stored as much carbon in the 30–45 cm layer as in the 0–15 cm surface layer. Additionally, the deeper soil profile (30–45 cm) was the only depth showing significantly increasing C stocks with time after abandonment ($r^2=0.21$; $p<0.001$). Considering all forests, total soil C to 45 cm depth increased non-significantly at a rate of 1.49 Mg ha^{-1} yr^{-1} during the first 12–14 yrs of succession (Table 4).

Total C accrual. In vegetation and soil (excluding roots), the ten SF accrued a total of 7.04 Mg C ha^{-1} yr^{-1} during the first 12–14 years after abandonment ($r^2=0.85$; $p<0.001$) (Table 4).

Discussion

Nutrient accrual

The vegetation withdraws large quantities of exchangeable Ca from low exchangeable soil reserves. After N, vegetation Ca stocks were accumulating most quickly with forest age. Wood and foliage N:Ca ratios were low, ranging from 0.7 to 1.4 for wood and 1.9 to 3.0 for foliage. In contrast, primary forest vegetation reported N:Ca ratios were 3.1 for trunks, branches and coarse roots, and 4.4 for leaves (Fernandes et al., 1997).

The high rate of Ca immobilization in vegetation but lack of reduced soil exchangeable Ca over time in our study indicates, (1) soils adequately replenish immobilized Ca from unavailable forms (Table 2); and/or (2) the vegetation is withdrawing Ca from deeper than 45 cm depth. A similar trend of a high percentage of total system Ca content in vegetation and high Ca uptake from low soil reserves of exchangeable Ca has been reported for temperate forests (Johnson and Henderson). The highly weathered Oxisols of our study provide negligible Ca from parent materials; however, atmospheric deposition may replenish depleted soil reserves by adding 0.8–12 kg ha^{-1} yr^{-1} (Vitousek and Sanford Jr., 1986; Schroth et al., 2001). For young tropical fallow vegetation, low root length density and low nutrient demand make Ca and nitrate ions susceptible to downward movement (Szott et al., 1999), which may be retrieved with increased rooting depth in later successional stages. Trees have been reported to increase soil nutrient availability over time (Sanchez et al., 1985) and net increases in total system stocks of N and Ca have been observed in older fallows, probably as a result of atmospheric deposition, N$_2$ fixation and uptake from subsoil (Szott et al., 1991). However, pasture soils were found to have higher exchangeable soil Ca concentrations than plantations, secondary and primary forests (McGrath et al., 2001), indicating that after the initial increase of soil Ca from cutting and burning, colonizing trees act as sinks, reducing soil Ca. Although soil Ca stocks are currently maintained in these SF, the high rate of Ca relocation from soil to vegetation, large vegetation Ca stocks, and high concentrations relative to N indicate extreme Ca demands for biomass production, which may create a soil Ca deficit and limit future vegetation growth.

The rapid total soil N stock and N concentration increase below 30 cm depth with forest age can be only partially explained by external inputs (Figure 1, Table 3). Nitrogen fixing plants may contribute 10–150 kg ha^{-1} yr^{-1} to soils (Fernandes et al., 1997; Szott et al., 1999) and atmospheric deposition may add 5.5–11.5 kg ha^{-1} yr^{-1} (Jordan et al., 1982; Vitousek and Sanford Jr., 1986; Schroth et al., 2001), explaining a fraction of the increasing total soil N. The remaining contribution to the high soil N accumulation rates could be subsoil mining of leached nitrate. Increasing extractable soil N with depth

below topsoil have been measured in young SF (J. Lehmann, pers comm.); high deep soil N concentrations may be attributable to leaching from surface layers after slash-and-burning and cropping, followed by a reduced nutrient capture potential of shallow rooted colonizing secondary vegetation. Primary forest also loses nitrate to the subsoil (Schroth et al., 1999). These large N pools were deep (1-2 m) and considered at the lower limit of uptake by young SF. Leaching of surface N can be rapid in Oxisols because of the high macroporosity and hydraulic conductivity, but leaching below 0.6 m is delayed, apparently because of NO_3^- adsorption to the net positively charged subsoil (Melgar et al., 1992). Deep nutrient pools may provide a source of N as forests mature and root systems develop. Leaching of surface N (0–15 cm) to deeper layers could also explain the increase in N concentrations (r^2= 0.75; p<0.001) we observed below 30 cm depth with forest maturation. Unless deep N mining occurs with root development, N losses to subsoil due to leaching may negatively affect surface soil fertility.

Compared to primary forest nutrient storage in soil (of the total aboveground and soil stocks), the SF stored comparable amounts of N, less P, but more Ca. Soil storage of exchangeable Ca and total N in the oldest SF accounted for an average of 26 and 89% of total nutrient storage, respectively, but just under 14% of extractable P (Figure 1). This contrasts with compartmentalization within primary vegetation, where soil storage of exchangeable Ca and total N may account for <1 and 73% of total nutrient storage, and extractable P in soil accounts for 69% of the total storage (Sanchez, 1987).

Increases in soil nutrient concentrations are followed by greater vegetation tissue concentrations in successional vegetation. Secondary forest vegetation growing on nutrient poor soil produced wood with three times less P and leaves with 50% less P than vegetation where soil P limitations were removed through P fertilizer additions (Gehring et al., 1999). The reduction in foliar P concentrations with increasing forest age observed in our study (Table 1) may indicate that this nutrient is becoming limiting as soil P levels decline (Figure 1).

Total aboveground and soil nutrient stocks increased as forests matured; yet, for P, uptake and soil P supply indicates a potential growth limitation. Concomitant decrease in extractable soil P and increase in biomass over time may be attributable to relocation from below- to above-ground pools. Plants appear to be taking up more soil P than is available (Table 2). This suggests a rapid transfer of soil P from plant unavailable to available forms or deep soil mining as the available pool is depleted with plant growth. However, subsoil P retrieval probably contributes <1 kg ha^{-1} yr^{-1} (Szott et al., 1999). The net reduction in soil P stocks from the soil (0.66 kg P ha^{-1} yr^{-1}) with increasing forest age, indicates inadequate replacement of available soil P with plant P uptake, a trend also observed elsewhere (Johnson et al., 2001). Should this trend continue, P may become limiting to growth unless other factors (1) reduce P uptake by plants, (2) increase P uptake from subsoil, (3) increase the rate at which unavailable forms of soil P shift to plant available P forms to replenish immobilized plant available soil P.

Pools of plant available (extractable) nutrients are significantly lower than the total in soils (Brown and Lugo, 1990), and the plant availability of the soil P depends on the extent of fixation or immobilization. Phosphorus fixation for Oxisols is lower in the central Amazon Basin than Oxisols in other regions of the Amazon; however, levels of plant available P in the soils are similar (Lehmann et al., 2001a). Total soil P in primary forest can be lower than under the SF replacing the vegetation (Lehmann et al., 2001b), indicating storage in biomass can significantly reduce soil extractable P stocks. Pastures grasses such as *Brachiaria* spp. may increase P availability by exuding acid phosphatase into the rhizosphere and hydrolyzing plant unavailable forms of organic phosphates (Dias-Filho et al., 2001), a benefit lost as secondary vegetation replaces the pasture grasses. Root associations with both VA-mycorrhizae and ectomycorrhizae may help the colonizing vegetation access P even at low soil P concentrations; and, in the case of ectomycorrhizae, to access P from poorly accessible pools (Boot et al., 1994). Since these colonizing species have the ability to take up P in excess of immediate growth requirements (Boot et al., 1994), P uptake by maturing trees may decline before plant levels become limiting to biomass accumulation. Fallow vegetation increased mineralizable N and available P compared to continuous cropping, probably as a result of deeper rooting (Tian et al., 2001).

Further research is needed to develop and evaluate management strategies that promote soil P acquisition, such as increasing rooting depth of regenerating vegetation.

Carbon accrual

Aboveground. Rapid biomass accrual in the SF, 11.0 Mg ha^{-1} yr^{-1}, was similar to other Amazonian findings (Uhl et al., 1988; Brown and Lugo, 1990; Alves et al., 1997), lower (Hartemink, 2001), and higher than a 20 year mean annual rate (6.17 Mg ha^{-1} yr^{-1}) in a review of tropical SF succession (Silver et al., 2000). The high C accumulation storage in the 12–14 yr-old areas represents 25–50% of equivalent primary forest biomass (230 – 500 Mg/ha) in Amazonia (Alves et al., 1997; Fujisaka et al., 1998; Laurance et al., 1999).

Aboveground carbon accrual slows with age as colonizing trees mature, die, and are replaced by slower growing species. Secondary forests in the Bragantina region of the Amazon basin were accruing biomass more rapidly in 10 yr-old (5.5 Mg ha^{-1} yr^{-1}) than in the 20–40 yr-old SF (3.3 Mg ha^{-1} yr^{-1}) (Johnson et al., 2001). And a review of 44 secondary tropical forests showed wet forests accumulating biomass significantly faster during the first 20 of 80 years of regrowth (Silver et al., 2000). Their rates through the first 10 and 20 years are still less than the rate we report through the first 12–14 years (Table 4).

Belowground. Our study indicates a trend of increasing soil C storage through the first 12–14 years (Figure 1); however, the soils are storing comparable to less C than other SF of similar or greater age (Silver et al., 2000); (Johnson et al., 2001). Although our forests only showed a weak C storage gain, other studies indicated that soil C storage (excluding roots) increases significantly with SF age, and can approach mature forests levels after 80 years regrowth (Silver et al., 2000).

Contrary to aboveground biomass accumulation rates, which proceed faster in SF following agriculture (Fearnside and Guimaraes, 1996), soils accumulate C almost twice as fast when regeneration follows pasture rather than agriculture, although this effect is only distinguishable after 20 years of recovery (Silver et al., 2000). Delays in aboveground C accrual with forest growth in early years following pasture abandonment may be offset, to a certain degree, by enhanced soil C accumulation.

Compared with soil C storage in pasture (49.5 Mg/ha; 0–30 cm depth) (Moraes et al., 1996), tropical plantation (90 Mg C/ha) and SF (61 Mg C/ha) (0–25 cm depth) (Silver et al., 2000), the SF soils in this study were storing 47.9 Mg C/ha to 30 cm and 66.1 Mg C/ha to 45 cm depth. Since aboveground C accrual appears higher than other sites, and soil C lower than other SF sites, high litter turnover and soil respiration rates at our sites may be reducing soil C residence time in this high rainfall area.

These factors pose important management implications to carbon sequestration. By choosing to maintain areas as pasture, directing SF colonization and succession after abandonment, or establishing plantations or agroforestry systems, land managers can influence the distribution of aboveground and soil C storage and the rate at which carbon accumulates within those pools. Maintaining the land cover as forest for longer time-periods rather than as degraded pasture is a more favorable practice to increase C storage.

Predictive limitations

The ≥1 cm DBH limitation imposed by the allometric equations may significantly underestimate biomass and nutrient stocks in the absence of root and biomass measurements of young SF vegetation <1cm DBH. Grasses tend to allocate a significant portion of total plant biomass within root structures (Nepstad et al., 1994) and necromass, shrubs and herbaceous vegetation dominating early pasture succession and SF understories contribute considerable quantities to C and nutrient stocks, especially P (McKerrow, 1992). Wood core measurements may overestimate nutrient concentrations in young stands since a greater portion of the sample core is nutrient rich bark. An underestimate of biomass as a result of DBH allometric limitations is inversely related to forest age. As stand dominance shifts from small- to large-stem diameter plants with understory shading and self-thinning, a greater percentage of the total stems are measured and contribute to biomass and nutrient calculations. Also, although we located our abandoned pasture study sites on plateaus, the pastures span the rolling topography. Nutrient limitations may be more severe on hillsides where erosion is more pronounced and forest recovery slower than the rates we predict.

Implications for succession, carbon sequestration, and nutrient barriers

After two and a half decades of neotropical studies of SF regeneration, we still lack the ability to make strong predictions about nutrient storage and successional shifts in forest development, and regeneration times for abandoned pastureland to attain primary forest equivalent biomass. This is largely due to an historic research focus on forest succession following agriculture rather than pasture. Since biomass recovery is significantly slower following pasture than agriculture (Fearnside and Guimaraes, 1996; Steininger, 2000), it is important to increase our understanding of pasture succession and determine potential nutrient limitations.

The paucity of forest recovery studies on abandoned pastureland and lack of detailed soil C and nutrient data make predicting forest regeneration on highly altered lands difficult. In a review of SF biomass accumulation (Silver et al., 2000), only 13% of the SF (18 of 134) were previously pastures. Additional data from SF regenerating from pasture are needed to determine long-term C accumulation rates, potential nutrient limitations to regeneration, and the time needed to attain both structural and functional properties of mature forests. This is especially relevant since primary forest biomass is positively associated with soil nutrient levels, suggesting that soil nutrient loss through pasture installation may result in lower mature regenerated forest biomass than the original forest (Laurance et al., 1999). Although studies such as ours help to fill this void, there is a need for long-term rather than chronosequential studies of forest recovery following pasture abandonment.

Summary

In this study, we show that during early successional years, biomass accumulation in light to moderately used pastures is rapid after abandonment and that soil C storage is higher in older forests. However, a slower soil C accrual rate than regenerating SF in other regions, may negatively offset total long-term C gains. The higher proportion of soil C storage compared to aboveground pools will be an important consideration of future 'carbon credit' management, as this pool is more recalcitrant to perturbations. Aboveground C re-accumulation from post-burn values is high, yet represents a finite pool which is rapidly attained in a relatively short time-period. Managing forest regeneration to maximize soil C storage, rather than aboveground pools, may prove to be more useful or meaningful when attempting to increase SF C sequestration.

Furthermore, the colonizing vegetation can extract large nutrient quantities from the soil, even when in low supply. There was not only a shift of nutrients from soil to aboveground pools, but total system nutrient stocks were increasing over time. Most of the C, N, and Mg were stored within soils, while P, K, and Ca resided within vegetation. This has important consequences to total forest nutrient stocks, in the event of removal of aboveground vegetation. In the absence of nutrient additions, removal of the vegetation a second time (pasture re-clearing or logging) could compromise the SF potential to regenerate as a result of nutrient limitations. Even after P fertilization when the areas were pasture, soil P stocks remained low. The vegetation was withdrawing more soil P than can be replenished, creating a soil P deficit which may limit system productivity. Low exchangeable soil Ca stocks seemed to be adequately replaced, apparently from atmospheric inputs and depths below 45 cm, as growing vegetation took up large nutrient quantities. Nevertheless, as vegetation Ca demands were high and soil stocks low, lack of Ca may limit future productivity.

These results demonstrate the regenerative capacity of tropical SFs to sequester C and to rebuild the nutrient capital following pasture abandonment. Aboveground carbon accrual is rapid but belowground gains represent the largest potential area for continued accumulation and management. Relocation of some nutrients from deeper soil layers may represent a substantial source of nutrients for plant growth and may be vital to sustaining long-term productivity and biomass accumulation. We recommend additional studies to explore P and Ca nutrient limitations to forest productivity and long-term measurements of soil nutrient fluxes and forest growth. Understanding nutrient limitations to resource capture will provide new options to manage forest regeneration and increase C accumulation on these globally important nutrient-limited soils.

Acknowledgements

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Slash-and-char – a feasible alternative for soil fertility management in the central Amazon?

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Abstract

The application of charcoal to nutrient-poor upland soils of the central Amazon was tested in lysimeter studies in comparison to unamended control soils to evaluate the effects of charcoal on plant nutrition and nutrient leaching. Testing the application of charred organic matter was stimulated by the fact that anthropogenic soils in the Amazon (so-called "Terra Preta") with high soil organic matter contents contain large amounts of pyrogenic carbon. These soils also show high cation exchange capacity and nutrient availability. Charcoal additions significantly increased biomass production of a rice crop in comparison to a control on a Xanthic Ferralsol. This increase was largely an effect of improved P, K, and possibly Cu nutrition, whereas N and Mg uptake decreased in charcoal amended soils. In order to improve crop growth, fertilizer applications of N, S, Ca, and Mg may be necessary in addition to charcoal for optimizing rice growth. Combined application of N with charcoal resulted in a higher N uptake than what would have been expected from sole fertilizer or charcoal applications. The reason is a higher nutrient retention of applied ammonium by the charcoal amended soils. Charcoal applications therefore acted in two ways, first as a direct fertilizer and secondly as an adsorber which retained N. The amount of charcoal which can be produced from forest biomass is significant and corresponds to charcoal amounts needed for effectively improving crop growth. The slash-and-char technique is an alternative to burning of the above ground biomass and only the biomass from the same cropping area will be used for charring. Field trials need to be conducted to investigate the efficiency of charcoal production and applications under field conditions.

Keywords: Amazon; Humid Tropics; Ferralsols; Leaching; Nutrient Cycling; Slash-and-Burn

Introduction

Upland soils in the humid tropics such as in the central Amazon are highly weathered and therefore possess low plant available nutrient contents (Cravo and Smyth, 1997). This is a result of both high rainfall and low nutrient retention capacity. Applied nutrients are rapidly leached below the root zone of annual crops (Melgar et al., 1992; Cahn et al., 1993). Two basic approaches can be used to reduce nutrient leaching, first to apply slow-releasing nutrient forms such as organic fertilizers or secondly to increase adsorption sites and thereby retain applied inorganic nutrients.

Slash-and-burn is one of the main land use system in the Amazon. Secondary or primary forest is cut and burned to clear the field but also to release plant-available nutrients from slashed plant biomass. The ash from the burned biomass increases soil pH and supplies nutrients to crops which show elevated nutritient levels and yields (Sanchez et al., 1983). This effect of the ash accumulation is, however, rather short-lived. Already after a few cropping seasons the soil nutrient availability decreases and field crops have to be fertilized for optimum production (Sanchez et al., 1983) or the fields have to abandoned and new forests have to be slashed and burned. Although adequate applications of mineral fertilizers were

shown to sustain yields in the Amazon (Smyth and Cassel, 1995), our efforts are intended to improve the use of biomass and nutrients contained in the plant biomass as well as that of applied fertilizer nutrients, since fertilization is expensive and crop production often has to rely on soil nutrients alone.

It is well known that about 50% of the carbon in the above ground biomass of forests can be lost upon burning (Kauffman et al., 1995). Sixty and 43% of the biomass N and S and 18, 7 and 7% of the P, Ca, and K were lost from the site (Kauffman et al., 1995). A large portion may be deposited or absorbed in surrounding ecosystems but does not contribute to the fertility of the cropped soil. The first approach should therefore aim at improving the efficiency of land clearing to preserve C and nutrients. Slash-and-mulch was successfully tested in Eastern Amazonia when fertilizer was applied (Kato et al., 1999) and has a long history in the per-humid tropics (Thurston, 1997). We are seeking an alternative technique that can be applied to the existing slash-and-burn system with minimal changes and that has the potential of being used in tree cultures as well.

Anthropogenic dark earths - evidence of sustainable soil management

Instead of burning the above ground biomass to clear the agricultural field, the biomass may be charred to produce charcoal and added to soil. Testing the application of charred organic matter was stimulated by the fact that anthropogenic dark earths in Central Amazonia (so-called "Terra Preta do Indio") with high soil organic matter contents contain large amounts of pyrogenic carbon (Glaser et al., 2001). These soils also show high cation exchange capacity, nutrient availability and organic matter (Sombroek, 1966; Kern and Kämpf, 1989). The origin of the dark earths is not entirely clear, and several conflicting theories were discussed in the past. Currently the most convincing theory states that these soils were not only used by the local population but a product of indigenous soil management as proposed by Gourou (1949).

Soil fertility increases have been observed on remnants of charcoal hearths in the Appalachian Mountains (Young et al., 1996). Tryon (1948) showed higher nutrient availability in clayey to sandy soils from the Western United States after additions of charcoal produced from conifer and hardwood. Coal from geological deposits were successfully tested for the improvement of soil physical properties (Piccolo et al., 1996). No information, however, is available about the effects of charcoal applications on nutrient availability of highly weathered soils in the humid tropics such as the central Amazon. It is also unclear whether the cation exchange capacity can be improved thereby leading to higher nutrient retention and to lower nutrient losses by leaching.

A slash-and-char technique does not advocate the destruction of existing primary forests. It should be a carbon- and nutrient-conserving alternative to existing slash-and-burn techniques. In this way, carbon will rather be retained in the system compared to slash-and-burn, since only the biomass from the same cropping area will be used for producing the charcoal.

Charcoal additions for soil fertility improvement

Experimental description

Pot experiment. A greenhouse study was carried out at the Embrapa Amazonia Ocidental near Manaus, Brazil. The mean temperature in the greenhouse was between 28-32ºC. We used two different soils for our experiments: (1) a Xanthic Ferralsol taken from a secondary forest (approximately 15 years old) with high clay contents (65%), medium organic C (39 g kg^{-1}) and N contents (31.7 g kg^{-1}); (2) a Fimic Anthrosol obtained from a farmers field under fallow with low clay (5%) and high sand contents (85%), high organic C (84.7 g kg^{-1}), available P (318 mg kg^{-1}) and Ca contents (656 mg kg^{-1}), but low to medium total N (49.6 g kg^{-1}), available K (4.0 mg kg^{-1}) and Mg contents (57 mg kg^{-1}). Both soils have not been fertilized prior to the experiment.

Free-draining lysimeters were constructed with a diameter of 0.2m and a height of 0.1 m which were filled with either 3 kg of the Ferralsol or the Anthrosol. The effect of soil type, mineral fertilizer and charcoal on growth, nutrient uptake and leaching was tested using rice (*Oryza sativa* L.) as a test plant.

Charcoal was applied at 20% weight which was produced by local farmers originating from secondary forests. The charcoal was ground by hand to a grain size of about 1 mm. Fertilizer was applied at 30, 21.8, and 49.8 kg ha^{-1} for N, P, and K using ammonium sulfate, TSP, and KCl, respectively. Lime was applied at 2.1 Mg ha^{-1} [all recommendations for rice from Araujo et al. (1984) Circular Técnica 18, Embrapa, unpublished].

After the soil was filled into the lysimeters, water was gently poured onto the soil at a daily rate of 6.85 mm (2500 mm y^{-1}). After four days the electrolyte content in the leachate had stabilized and fertilizer was added and rice was planted (five stands per pot with three plants per stand). Water was applied and drained daily, but only selected samples were analyzed. Nutrient contents were determined daily for the first week, twice a week for three weeks and after 5 and 10 days. The sampling was stopped when the rice was cut at 37 days after planting. The amount of leachate was determined by weight and a subsample was retained for further analyses and frozen. Cumulative leaching for the entire experimental period was calculated from the measured leachates and amounts were interpolated linearly. Plant samples were dried at 70ºC for 48 hours and weighed.

In a second pot experiment, seedlings of *Inga edulis* were planted in pots with 26 cm diameter and 10 dm^3 soil (Xanthic Ferralsol) in four replicates. Charcoal was added at 0, 1, 5, 10, and 20% weight corresponding to 0, 13.3, 66.7, 133.4, and 266.7 Mg C ha^{-1} (C concentration of charcoal 70.8%). Fertilizer was applied at 100 kg N ha^{-1}, 50 kg P ha^{-1}, and 60 kg K ha^{-1} as urea, triple super phosphate and KCl, respectively. Additionally, 2 Mg ha^{-1} lime were added. Stem diameter was determined at 5-cm above soil level, and tree height was measured including the length of the uppermost leaf at 80 day after planting.

Adsorption experiment. In a laboratory experiment, we studied the adsorption of different nutrients by charcoal. The charcoal was made from the wood of black locust (*Robinia pseudoacacia*). Cubes of dried wood with 10 g were isothermically combusted in closed metal containers at 350ºC for 40 minutes (65 replicates). Wood and charcoal were weighed with an accuracy of 0.1%. The charcoal was ground coarsely with mortar and pestle to pass a 2 mm sieve. One gram of charcoal was added to 10 mL of solution containing 0, 20, 50, 100, 200 mg L^{-1} using 20-mL PE bottles. In a preliminary experiment, the adsorption dynamics were determined for 10, 30 minutes, 1 and 6 hours, 1 and 3 days and 1 week using a horizontal shaker. Adsorption changed until one day, but did not differ thereafter. Therefore, adsorption experiments were done with a shaking time of one day. The effect of coating with dissolved organic matter (DOC) was tested with a manure extract. Ten grams cow manure were shaken with 20 mL deionized water and filtered. The filtrate was diluted 50 times and 10 mL of the solution was shaken with 1 g of charcoal for 24 hours. Afterwards the same adsorption experiment with different concentrations only of NH$_4^+$ was performed as described above with and without additions of 10% azide to inhibit microbial activity.

Chemical analyses. The aboveground biomass of rice was ground with a ball mill and analyzed for nutrients and organic carbon. C and N analyses were performed with an automatic CN analyzer (Elementar, Hanau, Germany). The K, Ca, Mg, Fe, Zn, Cu contents in the plant biomass were determined after wet digestion with sulfuric acid using atomic absorption spectrometry (AA-400, Varian Associates, Inc., Palo Alto, CA). The P contents were measured photometrically in the same extract with the molybdenum blue method.

The K, Ca, and Mg contents in the leachate and adsorption solution were measured using atomic absorption spectrometry, nitrate (NO$_3^-$) and ammonium (NH$_4^+$) concentrations were determined photometrically with a continuous flow analyzer (RFA-300, Alpkem Corp., Clackamas, OR and Scan Plus analyzer, Skalar Analytical B.V., Breda, The Netherlands) after reduction with Cd and reaction with salicylate, respectively.

Statistics. Treatment effects of the bioassay were analyzed by analysis of variance (ANOVA) with a randomized complete block design. Mean separation was done using the least significant difference test (LSD).

Charcoal as a fertilizer

Charcoal additions increased biomass production of a rice crop by 17% in comparison to a control on a Xanthic Ferralsol (Figure 1). This increase was largely an effect of improved P, K, and possibly Cu nutrition. Nitrogen and Mg uptake decreased in charcoal amended soils which resembled the uptake pattern of rice grown on an Amazonian dark earth (Fimic Anthrosol; Figure 1). Charcoal additions had no significant effects on S, Ca, Fe, Zn, and Mn uptake (P>0.05). In addition to charcoal, fertilization was necessary with N, S, Ca, and Mg for optimizing rice growth.

The soil fertility improvement of the dark earth was largely an effect of enhanced P, Ca, and micronutrient availability such as Mn and Cu. Crop nutrition of S and K was not better and that of N and Mg was even lower in rice grown on a dark earth in comparison to the Ferralsol. Fertilization was necessary for those elements and was effective in increasing total nutrient uptake (Figure 1).
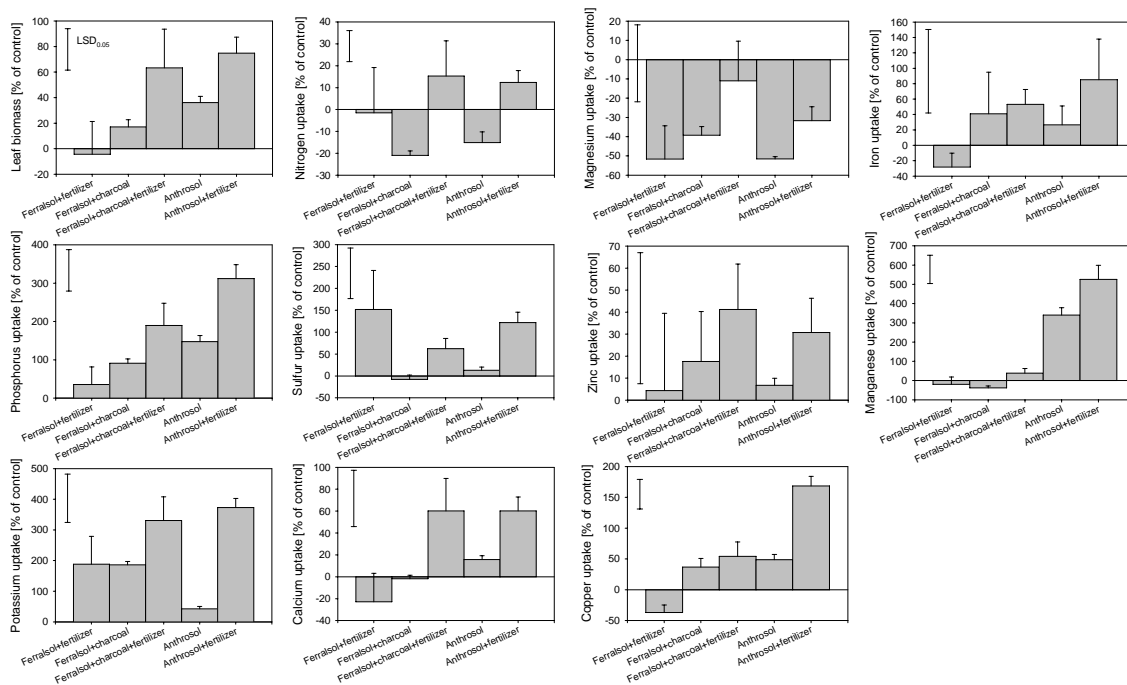

Figure 1: Biomass production and nutrient uptake by rice (*Oryza sativa*) after additions of charcoal and fertilizer to a Xanthic Ferralsol or a Fimic Anthrosol after 37 days (means and standard errors; N=4).

Therefore, charcoal directly amended the soil with plant-available nutrients such as P, K, and Cu. If fertilizer was applied together with the charcoal some nutrients showed a higher uptake efficiency than the added effects of fertilization and charcoal amendment would suggest. This was the case for N, Ca, and Mg. In the following we discuss the reasons for a higher efficiency of a combined application.

Charcoal as an adsorber

Under the high leaching conditions in upland soils of the central Amazon, reduction of nutrient losses by leaching is an important aim in order to improve nutrient availability for plants. Immediately after fertilizer application, nutrient contents significantly increased as shown for ammonium (Figure 2) and leveled off to background levels only 21 days after fertilization. This was also the case with K, Ca, and Mg (data not shown).

Leaching from the unfertilized Ferralsol was reduced when charcoal was applied and resembled the low values found in the Anthrosol (Figure 2). Ammonium concentrations in the leachate were also significantly lower in the fertilized Ferralsol after charcoal applications. These results indicate that ammonium was adsorbed by the charcoal and elevated N uptake by rice after the combined application of charcoal and fertilizer (Figure 1) was an effect of ammonium retention. This retention could not be found for other cations or anions, because K, Ca, and Mg were in higher supply with charcoal additions. After several cropping cycles, the nutrients in the charcoal may be depleted and results may differ from those shown here. Since N was applied as ammonium, nitrate contents in the leachate were controlled by biological transformation rather than physical adsorption.
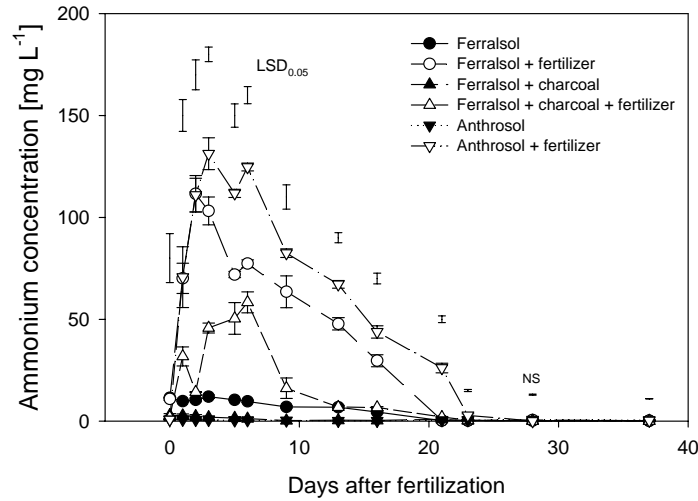

Figure 2: Ammonium concentration in the leachate of a Xanthic Ferralsol amended with charcoal and fertilizer compared to a Fimic Anthrosol; main effects significant at P<0.001 apart from one (NS not significant P>0.05) (means and standard errors; N=4).

In accordance with the leaching results, only ammonium was adsorbed by charcoal (Fig. 3) whereas all other nutrients (P as PO_4^{2-}, Ca, Mg, K) showed higher concentrations in the equilibrium solution than added (data not shown). The process of adsorption is largely a co-adsorption with soluble organic matter, as an addition of dissolved organic carbon (DOC) from a manure extract increased ammonium adsorption. A microbial immobilization or nitrification during shaking can be excluded, since the adsorption was similar when microbial activity was suppressed by additions of azide (Fig. 3).
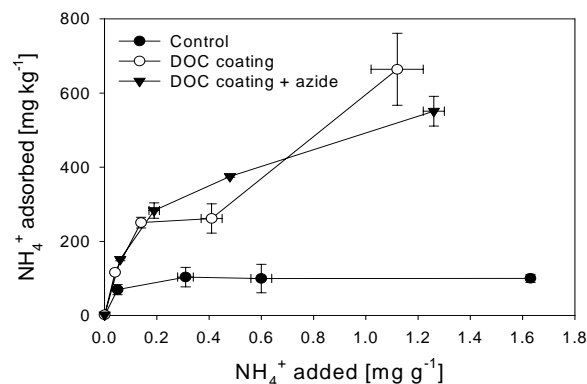
Figure 3: Ammonium adsorption by charcoal produced from black locust (*Robinia pseudoacacia*) in comparison to charcoal coated with manure or additional suppression of microbial activity using 10% azide (means and standard errors; N=2).

Slash-and-char in smallholder agriculture

If a slash-and-char technique was to be successful, (i) the quantity of applied charcoal must be produced from the same area of land that is cropped, and (ii) the periods of charcoal production must at least correspond to those of land clearing practiced so far. In other words, the slash-and-char technique must work with the same resources as conventional methods and be an alternative to slash-and-burn or slash-and-mulch. The amount of charcoal which can be produced from different forest vegetation primarily depends on the woody biomass available, and additionally on the production procedure such as charring environment (e.g., oxygen), temperature and time (e.g., Glaser et al., 2002). The average recovery of charcoal mass from woody biomass is 31% according to the published data compiled in Table 1. The effect of different charcoal production methods on its recovery in agricultural fields is not well known and the charring environment such as temperature and charring time is usually poorly documented. The carbon contents of charcoal do not vary much and lie around 63-83% with a mean of 76% (Table 1). The carbon recovery from charred woody biomass is relatively high with 54% (Table 1) due to the high carbon contents of charcoal.

Several published values of above ground biomass from secondary and primary forests in the central Amazon show a high proportion of woody biomass (Table 2). Biomass of secondary forests increase with age but depend largely on site conditions and previous land use. Larger amounts of charcoal can be produced from primary (57-66 Mg C ha^{-1}) than secondary forests calculated with the average conversion from Table 1. But also secondary forests may produce charcoal equivalents of up to 32 Mg C ha^{-1} after only 4 years (Table 2). The pot experiment shown in Figures 1 and 2 was conducted with a charcoal amount of 135 Mg C ha^{-1} (20% weight in 10 cm depth), but also 67 Mg C ha^{-1} (10%) were shown to significantly improve biomass production of cowpea (Lehmann et al., unpublished). In a pot experiment with *Inga edulis*, tree height and stem diameter significantly increased through the addition of charcoal (Figure 4; ANOVA P=0.041 and 0.007, respectively). Already at the lowest application rate (13.3 Mg C ha^{-1}), charcoal additions were equivalent to fertilizer applications. Therefore, the charcoal amounts produced from the same area of land which is used for cropping during one charring event are sufficient for improving crop performance and for reducing nutrient leaching. Lower amounts of 7.9 Mg C ha^{-1} were shown to have only minor effects on rice yield in the first cropping season under field conditions (Steiner and Nehls, unpublished data) but more information is needed from field experiments. With increasing charcoal additions, growth of *Inga* decreased when no fertilizer was applied but increased with fertilizer applications.

Table 1: Biomass conversion into charcoal

Tree species	Charring temperature [°C]	Production method	Charcoal recovery by weight [%]	n	Charcoal carbon content [%]	Carbon yield[1] [%]	Source
Acacia mangium	450	laboratory furnace	37.9	60	76.4	64.4	Lelles et al. (1996)
Eucalyptus grandis	470	laboratory furnace	33.8	60	80.7	60.6	Vital et al. (1986)
Eucalyptus camaldulensis	450	laboratory furnace	32.4	25	76.3	54.9	Vital et al. (1994)
Deciduous trees	500	laboratory furnace	30.2	8	84.7	56.8	Zhurinsh (1997)
Pinus sylvestris (sawdust)	300	laboratory furnace	21.6		62.8	30.1	Glaser et al. (1998)
Robinia pseudoacacia	350	laboratory furnace	33.2	65	71.3	52.6	this study
Leucaena leucocephala	not given	metal kiln	27.4		83.1	50.6	San Luis et al. (1984)
Coconut trunk	not given	metal kiln	25.0		77.8	43.2	San Luis et al. (1984)
Mixed tropical wood, Manaus, Brazil	not given	brick kiln	41[3]		74.8	68.2	Correa (1988)
Miombo woodland[2]	not given	earth kiln	23.3		n.d.	-	Chidumayo (1991)
Mixed tropical hardwood	not given	earth pit	nd		69.0	-	FAO (1985)
Average			**30.6**		**75.7**	**53.5**	

[1] Percentage of charcoal carbon from the carbon in wood. Assuming 45%C in wood; determined for *R. pseudoacacia* at 45.7%.

[2] Total conversion of 93% of the woody biomass from a miombo woodland, representing 97% of the total above ground biomass.

[3] Calculating a conversion of 16 m^3 to 9 m^3 with a density of 0.7 and 0.51 Mg m^{-3} for wood and charcoal, respectively.

Charred organic matter from leaves was not accounted for in the calculation and the conversion to charcoal is currently not known. The contribution of leaves to charred organic matter from secondary or primary forests may be small, however, since the proportion of leaves in these forests usually lies below 10% (Table 2). Nevertheless the contribution to total nutrient input may be significant and has to be considered in nutrient budgets

Table 2: Above ground live biomass of secondary and primary forests in the Amazon.

Region	Type	Age of forest	Total above ground biomass [Mg ha⁻¹]	Woody biomass [Mg ha⁻¹]	Wood C content[1] [%]	Charcoal yield from biomass[2] [Mg C ha⁻¹]	Source
Rondonia and Para	2nd regrowth	4	134.2	119.6	49.6	31.7	Hughes et al. (2000)
Rondonia and Para	3rd regrowth	4	90.6	72.7	49.6	19.3	Hughes et al. (2000)
San Carlos, Venezuela	Secondary forest	5	40.1	35.2	nd	8.5	Uhl and Jordan (1984)
Paragominas, Para	Secondary forest[3]	3.5	16.3	12.9	nd	3.1	Buschbacher et al. (1988)
Paragominas, Para	Secondary forest[3]	8	35.0	30.4	nd	7.3	Buschbacher et al. (1988)
Paragominas, Para	Secondary forest[4]	8	86.5	81.8	nd	19.7	Buschbacher et al. (1988)
Zona Bragantina, Para	Secondary forest	2.3	22.2	16.5	nd	4.0	Gehring et al. (1999)
Zona Bragantina, Para	Secondary forest	10	54.9	49.8	47.3	12.6	Johnson et al. (2001)
Zona Bragantina, Para	Secondary forest	20	65.5	59.2	47.9	15.2	Johnson et al. (2001)
Zona Bragantina, Para	Secondary forest	40	128.8	119.8	47.6	30.5	Johnson et al. (2001)
Manaus, Amazonas	Primary forest	-	264.6	251.2	48.9	65.7	Fearnside et al. (1993)
Altamira, Pará	Primary forest	-	262.5	222.3	49.1	58.3	Fearnside et al. (1999)
Ariquemes, Rondonia	Primary forest	-	272.2	260.0	44.4	63.5	Graça et al. (1999)
Belem, Para	Primary forest	-	256.7	247.6	48.8	59.9	Mackensen et al. (2000)
Zona Bragantina, Para	Primary forest	-	229.6	225.1	47.3	57.0	Johnson et al. (2001)

[1] Where no information was available, C contents were estimated at 45 %.
[2] Calculated using the mean conversion of wood biomass to charcoal from Table 1.
[3] With previous pasture use of moderate intensity.
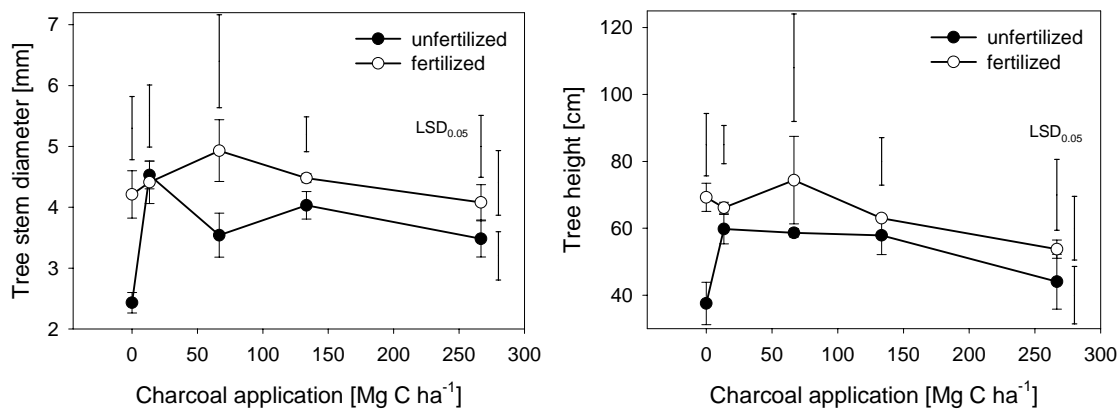[4] With previous pasture use of low intensity.

Figure 4: Tree growth of *Inga edulis* seedlings in pots amended with mineral fertilizer and increasing amounts of charcoal after 80 days (means and standard errors; N=4; Rondon et al., unpublished data).

Conclusions

Charcoal applications directly increased nutrient availability such as P and K and additionally increased nutrient retention for ammonium. Whether a net nutrient retention of other cations occurs after excess nutrients have been leached or taken up by plants remains to be shown. In this respect the long-term dynamics of soil fertility with charcoal applications are very interesting in comparison to burning or mulching. It may be assumed that nutrients bound to charcoal are more persistent than those in ash or mulch but direct evidence needs to be gathered.

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Effects of Land Use Change in the Llanos of Colombia on Fluxes of Methane and Nitrous Oxide, and on Radiative Forcing of the Atmosphere

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Abstract

The Colombian savanna (Llanos), covers 26 million hectares and is one of the few remaining frontiers where agriculture can expand. Current land use includes native savanna vegetation on clay-loam and on sandy-loam Oxisols, gallery forest, introduced improved pastures and cropland. Little is known about the fluxes of greenhouse gases in this ecosystem. Here we report field measurements of fluxes of methane and nitrous oxide for various land uses and estimates for their annual budgets in the Llanos. Emission of greenhouse gases due to burning of native vegetation and the contribution of methane emissions by termites and cattle have been included to estimate the radiative forcing potential of the atmosphere (global warming potential) for the Llanos.

Soils under pastures were found to be net annual sources of methane, while soils under other land uses were net annual sinks via methane oxidation. Soils under gallery forest showed the highest methane sink. Soil texture influenced fluxes of GHG. Annually, sandy-loam soils oxidized more methane than clay-loam soils (both under native vegetation). Soils of the Llanos were estimated to oxidize 6.4Gg/y of methane. Soils of the gallery forest covering 10% of the area of the Llanos, represent 48% of total methane sinks. All soils were minor sources of nitrous oxide with land under upland rice cultivation having the highest emission rates due to the input of fertilizer-N or green manure. Net emission by soils was estimated to be 12.4 Gg/y and soils were the major factor in the nitrous oxide budget of the region.

Annual emission of CH_4 by cattle (0.10Tg) is the main single source of this gas in the Llanos followed by direct emissions from biomass burning (0.06Tg/y). Termites contributed very little to net methane emissions.

Considering the main sources and sinks of trace gases, it was estimated that the Llanos is a net source of 0.164 Tg CH_4/y and 0.021 Tg N_2O/y. For a 20-year time horizon, the global warming potential of the Llanos under current land use distribution is 22.2 Tg CO_2 equivalents which is less than 0.005% of estimated global planetary radiative contribution. Therefore, the Llanos can be considered as an "environmentally friendly ecosystem". The doubling in area under improved grass-legume pastures and cropland expected by the year 2020 will reduce this contribution to 16.5 Tg CO_2 equivalents, mainly due to the reduction in emissions from biomass burning and to CO_2 sequestration as soil organic carbon by deep-rooted grasses.

Introduction

The Eastern plains (Llanos) of Colombia cover an area of 26 million ha and are the only land in Colombia available for agricultural expansion. The climate is sub-tropical with distinct wet and dry seasons. The natural landscape is a mosaic of grass covered, rolling savanna dissected by numerous rivers and streams that are bordered by evergreen gallery forest. Small termite mounds are abundant in the grasslands. The gallery forest accounts for nearly 10% of the total area (Rippstein and Girard, 1995). Low soil fertility and frequent natural or induced fire prevent forest from re-colonizing the land (Rippstein et al., 2001). Over the past two centuries the native grassland has been grazed by low productivity livestock and currently supports 3 million cattle (Rivas, 2000).

The soils of the Llanos are very acid (pH <4.3) Oxisols (Typic Haplustox), low in nutrients and very high in aluminum saturation (>80%). There are two contrasting textural groups; approximately 90% of the soils are clay-loams and 10% are sandy-loams. The soils are generally poorly drained and prone to compaction that can be induced by tillage or by cattle trampling (Amézquita, 1998). Despite these limitations, agricultural activities have intensified in the region during the last decade. Oil palm, rice, maize, soybeans, sorghum and improved pastures are now appearing, especially in the vicinity of the main cities and connecting roads. Intensification will be accelerated in the coming decades and various crops and management strategies have been developed to allow sustainable use of the Llanos (Friesen et al., 1997). The most promising among these are improved pastures with mixtures of grasses (e.g, *Brachiaria sp.*) and forage legumes (e.g. *Desmodium ovalifolium, Arachis pintoi, Centrosema acutifolium*), and rotations of cowpea or soybeans as green manures with varieties of upland rice or acid tolerant maize (Friesen et al., 1997b).

The Llanos is a complex ecosystem from the perspective of exchange of greenhouse gases between the land and the atmosphere, and agricultural intensification can be expected to have a large impact on these exchanges. In the natural system, fire and termites cause emissions of CO_2, CO, CH_4, NO, N_2O and volatile organic compounds to the atmosphere (Delmas, 1997;). Cattle are important sources of CH_4 and forage quality has a large impact on the amount of CH_4 emitted per unit of live weight gain or milk production. Soils are sources or sinks for carbon, N_2O and CH_4. Improved pastures have shown major increases in carbon stocks in soils of the Llanos (Fisher et al., 1994). Several studies in temperate ecosystems have found that the conversion of natural lands to agriculture may reduce oxidation rates of CH_4 and/or increase emissions of N_2O by soils (Sitaula et al., 1995; Mosier et al., 1991; Davidson et al., 1995, Willison et al., 1995). High doses of N-fertilizers stimulate N_2O emission but can reduce CH_4 oxidation (Bronson and Mosier, 1994). Less information is available for soils of the tropics; Nobre (1995) found that the conversion of native Cerrados in Brazil to high input agriculture increased N_2O emissions by a factor of ten relative to natural environments. On the other hand, Lauren et al. (1995) found little impact of land conversion to pasture or cropland on CH_4 and N_2O fluxes from a soil near Brasilia. Soils at this site were net sinks for atmospheric CH_4 throughout the year and oxidized from three to six times more CH_4 than similar land uses in temperate regions. Emission rates of N_2O were very low compared to temperate system counterparts. Venezuelan savannas are believed to be small net sources of CH_4, although only short-term measurements have been reported (Sanhueza et al., 1995).

Changing land use in the Llanos will influence more that one of the factors responsible for exchange of greenhouse gases with the atmosphere. Conversion of savannas to pastures or cropland eliminates fire and reduces the population of termites, thereby reducing emissions of CO_2, CO, CH_4, NO, N_2O and volatile organic compounds. Improved pastures will enhance carbon sequestration in soils and the higher quality forage will reduce emissions of CH_4 per unit of production. However, improved pastures also allow higher stocking rates, leading to increases in CH_4 emission by cattle per unit area of land. Conversion of land to cropland is expected to reduce the soil CH_4 sink strength and increase N_2O emissions. The objectives of this study were to assess annual fluxes of N_2O and CH_4 for the main land uses found in the Llanos, to use this and other data to make estimations of the radiative forcing potential (Global Warming Potential (GWP)) of this ecosystem under current conditions and to predict the effect of expected changes in land use over the next two decades on regional GWP. Results can be used to inform policy makers on decisions affecting the future development of the region.

Materials and Methods

Experimental Sites
Field research was conducted at the Corpoica-CIAT Carimagua station, in the middle of the Colombian Llanos (4° 37' N latitude; 71° 19' longitude). The altitude is 175 masl, and annual rainfall and mean temperature were 2498 mm and 28°C respectively for the period of the study (Nov 1997 to Dec 1998). Oxisols of two contrasting textures, a clay-loam (18% sand, 47% silt, 35% clay) and a sandy-loam (64% sand, 17% silt, 19% clay), typical of the Llanos were used in this study.

Six study sites representing native and agricultural systems were chosen. Four sites were selected from treatments in a long-term agro-pastoral/crop rotation experiment that was established on a clay loam soil in 1992 to evaluate the sustainability of several cropping and management systems in the Llanos. Details of the experiment are presented elsewhere (Friesen, 1996). The systems used were: native savanna, legume-grass pasture (B. *dictyoneura* + *A. pintoi*), upland rice as a monocrop and upland rice in a rotation with cowpea as green manure. Experimental plots were strips 20-m wide by 200-m long. A native savanna site on a sandy-loam soil (30-km southwest of the main site) and gallery forest site (9 km to the north of the main site) on a clay loam soil were also studied.

Soil properties

A detailed characterization of soil physical and chemical parameters to a depth of 30 cm was performed in May 1998. Bulk density was measured by the sand replacement method and resistance to penetration by a cone penetrometer. Both parameters were measured using procedures described by Smith and Mullins (1991). Four replicate undisturbed core samples were taken at 5-cm depth increments for determination of air permeability following the method of Koorevaar (1983). Samples were collected in metal cylinders (5-cm diameter, 5-cm height) that were capped immediately after collection. Saturated hydraulic conductivity, particle size distribution, soil porosity and pore size distribution were measured as described by Smith and Mullins (1991) and susceptibility to uniaxial soil compaction as described by Culley (1993). Chemical parameters measured were pH (water 1:1), soil organic matter (wet combustion), N content (micro Kjeldahl), and available P (Bray II). Chemical analyses followed the procedures of Hendershot et al. (1991). In April and October 1998, levels of nitrate and ammonium were determined in samples collected down to 1-m depth.

Gas Flux Measurements

The vented closed chamber technique (Conen and Smith, 1998; IAEA, 1992) was used to monitor fluxes of CH_4 and N_2O between the soil and the atmosphere. Four replicate PVC rings (10-cm high by 30-cm diameter) per treatment were permanently inserted 7-cm into the soil. White polyethylene vented chambers (10 cm high and 30 cm diameter) were attached to the rings just prior to each 1-hour measurement period. A 5 cm wide rubber band cut from a tire innertube was used to seal the joint between the chamber and the ring. The top of a chamber was fitted with a septum to facilitate extraction of gas samples, a hole for insertion of a digital thermometer, and a venting glass tube to prevent pressure differentials between the chamber and the atmosphere. The dimensions of the venting tube (0.5 cm diameter, 8 cm high) were selected as described by Hutchinson and Mosier (1981), and the tube was inserted 5 cm inside the chamber.

To reduce temperature increases within chambers, a reflecting white cover was placed over the chamber during the period of sampling. Gas samples were collected in 20 mL teflon-valved glass syringes at 0, 20, 40 and 60 minutes after installing the chamber. Immediately after collection, 15 mL of gas were transferred to high vacuum pre-evacuated glass containers (10 mL in volume). The glass containers were pre-evacuated to $2-3 \times 10^{-6}$ mbar, using a freeze dryer that also allowed capping of the evacuated vials with butyl rubber caps, which are impermeable to CH_4 and N_2O (IAEA, 1992). An aluminum over-cap was crimped over the rubber cap to effectively seal the flask and avoid accidental opening. Preservation of samples in these containers was found to be longer than 6 months, however analysis of samples was always completed within four weeks of collection.

At the time of gas sampling, composite soil samples (0-10 cm) were collected from around each chamber for determination of moisture content. Soil temperature was measured within the area of the chamber just before and after the sampling period. Air temperature inside the chamber was recorded at every sampling interval to later account for the change in the density of the air inside the chamber as a function of temperature. Gas flux measurements were initiated on November 1997. Sampling frequency was at three-week intervals, except for the first month when three samplings were made. The order and time of sampling was standardized; sampling was started at 8 am, 9:30 am, 11 am and 2:00 pm for the

sites under clay-loam savanna, rice, rice-cowpea and pasture respectively. Samples from the sandy-loam savanna and the gallery forest were collected the next day beginning at 10 am and 3 pm respectively.

A Shimadzu model 14A gas chromatograph (GC) equipped with FID and ECD detectors was set up to simultaneously analyze CH_4, N_2O and CO_2 in the same sample, while venting N_2, O_2 and H_2O (Rondón, 2000). A 14 port, two-position valve (Valco Instruments) was used to inject samples via a 2-mL gas loop and to re-direct the stream of gas to the ECD detector just after the CH_4 peak was obtained with the FID detector. The system used a pre-column (1-m) and a main column (3-m), both were 1/8 inch stainless steel tubing filled with Porapaq Q (80-100 mesh), and a carrier gas (N_2) flow rate of 25 mL min⁻¹. An electrically operated pneumatic actuator was used to precisely time the switching of the valve. CLASS VP software (Shimadzu) was used to control the actuator as well as the GC. The GC temperatures were 24°C at injection port, 60°C for the columns and 320°C for the ECD detector. For each gas sample, a 3 mL sub-sample was withdrawn from the glass vials using a 5 mL glass syringe fitted with a Teflon valve and injected into the GC via the sample loop. The existence of positive pressure inside the vials was checked at the time of sample withdrawal. Analysis time per sample was 5.5 minutes. Gas retention times were 2.1 minutes for CH_4, 3.8 min for CO_2 and 4.8 minutes for N_2O. Class VP software was used to calculate the concentrations (ppm) of the gases relative to the standards. Compressed air and Scotty prepared mixtures containing 1 and 3 ppm CH_4 and 0.9 and 5 ppm N_2O were the most commonly used standards. For samples high in CH_4 or N_2O, other standards were used (i.e. 10, 100 ppm CH_4 and 10, 100 ppm N_2O) as appropriate.

Gas Flux Calculations and Statistical Analysis

Differences in gas concentrations over time were used to calculate gas flux to/from soil for each chamber using the condition of a linear increase for at least three points to accept a flux measurement. When the linearity condition did not occur, the four samples were reanalyzed and the chamber was not considered in the calculations of flux averages if the problem persisted. For CH_4, fluxes are shown as net oxidation rates (net CH_4 consumption by the soil) with emissions from soil shown as negative values. For N_2O, positive fluxes represent emissions from soil. Annual fluxes were estimated by integrating the net area under the curve for the plot of gas flux over time. The method was applied to each of the four chambers in every land use, in order to calculate the reported average value. Annual fluxes represent the balance between periods of net emission and net consumption.

Comparisons of annual flux averages between land-uses were made by one-way analysis of variance using SYSTAT version 8 software. Comparison of means was done using Tukey's HSD method. A level of significance of ≤5% was used.

Results and Discussion

Environmental and Soil Parameters

Weekly rainfall and minimum, maximum and average temperatures for the period of measurement are shown in Figure 1. Annual rainfall in the study year (2323 mm) was slightly higher than the 20-year average for the station (2150 mm). March was also wetter than usual while September was drier than usual. In general, the Llanos has a dry season from November to April and a wet season from May to October. A clear alternation of dry and wet days is common in the rainy season, which helps to prevent the soil from becoming waterlogged for long periods of time. The number of days without rainfall (222) exceeded that of rainy days (142) during the year. Towards the end of the dry season, strong solar radiation and frequent winds dried grassy vegetation. Deep rooted shrubs and the gallery forest, with the ability to extract water from deep in the soil, remained green throughout the year. Temperatures are fairly constant through the year with a maximum daily variation of 10°C. For most of the day, temperature remains in a narrow band from 26-29°C. No significant correlation was observed between air temperature and gas fluxes.
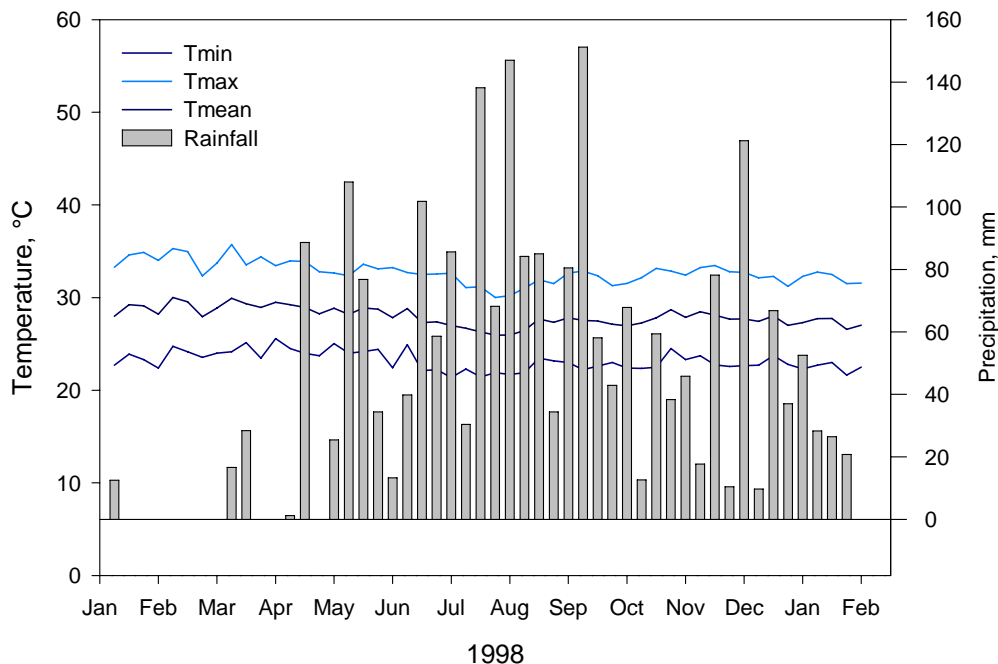
Figure 1. Weekly precipitation, maximum, minimum and average temperature at Carimagua Research Station. Tropical savannas of Colombia

The annual variation in soil water content, expressed as % water filled pore space (WFPS), in the top 10 cm of the soils is shown in Figure 2. The sandy-loam soil clearly has an intrinsically lower water retention capacity than the clay-loam soil and became extremely dry during the dry season (Figure 2A). Soil under the forest tended to be slightly drier than the clay loam savanna soil during the rainy season and slightly wetter during the dry seasonThis difference is likely a result of the combination of higher organic matter content (Figure 3G) and associated higher total porosity (Figure 3D) in the forest soil, together with reduced evaporation, as the soil is not directly exposed to sunlight. Soil under the pasture consistently retained more moisture than soils under other land uses (Figure 2B) and the difference is accentuated during the peak of the rainy season (June to August). Other studies have also found that pastures tend to retain more water than other land uses on the same soil (Roth, 1999; Keller et al., 1993). Water content in the cropped soils was very similar to that in the clay loam savanna, although laboratory measurements indicated that the amount of water that could be retained in the plow layer was reduced by cultivation (Figure 3B). Figure 3B also shows that conversion of land from savanna to pasture increased soil water retention capacity.
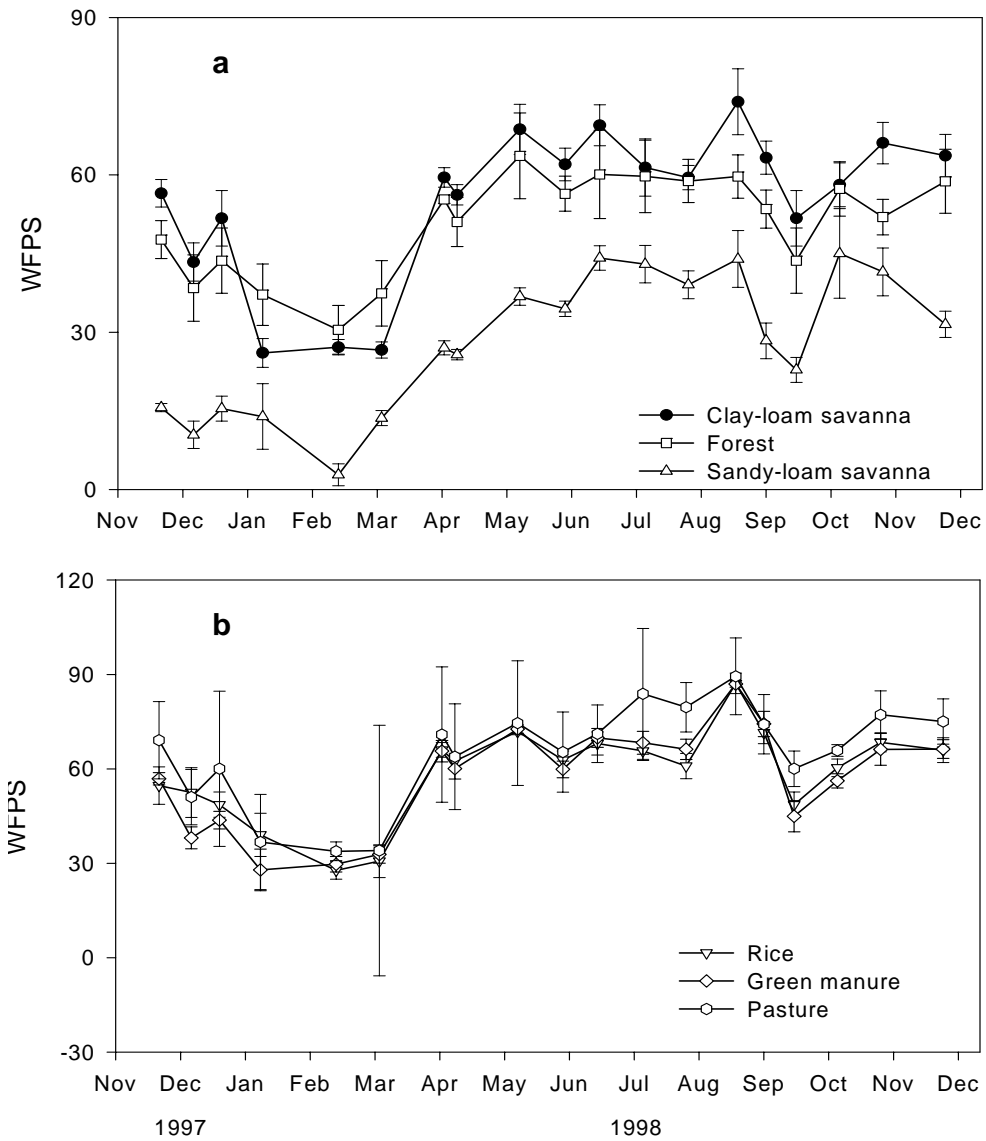
Figure 2. Water filled pore space (WFPS) in soils under various land uses in the Llanos
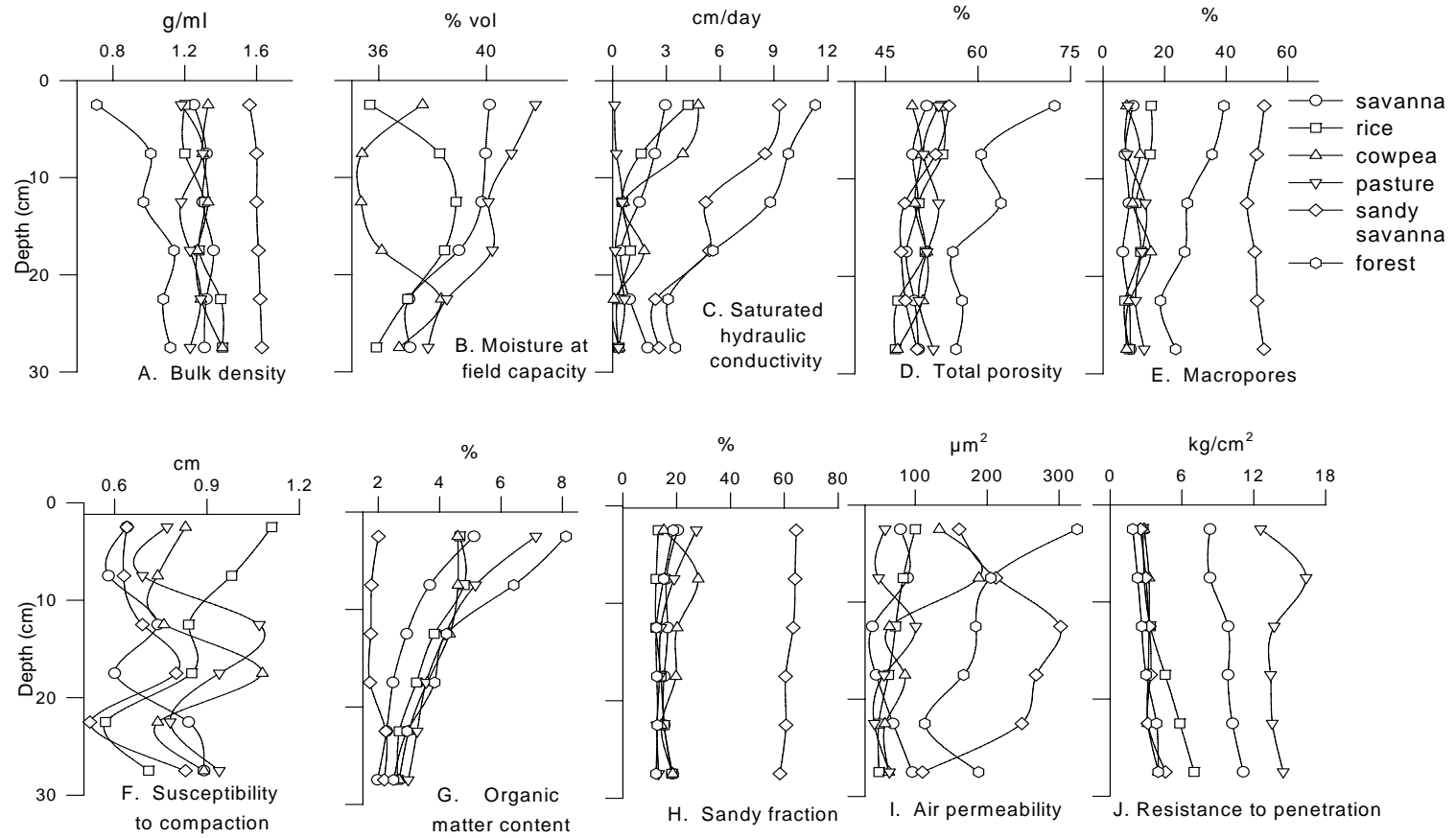
Figure 3. Selected soil properties for various land uses in Colombian savannas

With the exception of the gallery forest soil, saturated hydraulic conductivity was generally low in the clay loam savanna soils, which explains the characteristic wetness of this environment. Poor drainage was exacerbated by conversion of savanna to pasture. Reduced water conductivity in the pasture (Figure 3C) is attributed to sub-surface soil compaction as can be seen from the increased resistance to penetration in the 5-10 cm depth (Figure 3J), probably as a result of cattle trampling. In fact, susceptibility to compaction (Figure 3F) is higher for the whole profile in the pasture compared to the corresponding savanna. Lower susceptibility values for the 5 to 10 cm and 20 to 25 cm layers of the pasture indicate that these layers are already compacted. Other researchers (Mosier and Delgado, 1997; Keller et al., 1993) have also reported subsurface compaction and increased water retention in pastures. As expected, hydraulic conductivity (Figure 3C) is higher in the sandy soils than in the clay-loam soils, demonstrating the influence of soil texture. The greatest hydraulic conductivity was found in the gallery forest soils, probably as a result of improved aggregation due to higher SOM contents, coupled with increased presence of root channels and faunal activity which, in turn, results in low soil bulk density values.

Fluxes of Greenhouse Gases

Methane
Methane oxidation rates from November 1997 to December 1998 for soils under native vegetation and agricultural use are shown if Figures 4A and B, respectively. The temporal variation in CH_4 oxidation rate is high, with average values ranging from +120 μg CH_4 $m^{-2}h^{-1}$ for the forest in December to -320 μg CH_4 $m^{-2}h^{-1}$ (net emission) for pastures, in August. Spatial variability within a land use was also high, with RSD values ranging from 10% to 400%. However, for most of the sampling dates, RSD was in the range 60 to 120%, which is comparable to other studies on similar soils in the tropics (Poth et al., 1995; Cofman et al., 1998; Scharfe et al., 1990; Keller, 1994). The highest spatial variability was found with soils under rice, while forest and sandy savanna soils showed consistently lower variability.

Methane fluxes followed distinct patterns according to rainfall and soil moisture regimes. During the dry season (November to April), soils under all land uses were net sinks for atmospheric CH_4. Oxidation of CH_4 was progressively reduced as the soils became wetter in the rainy season (May to October). Soils of the clay loam savanna and the pasture eventually became a source of CH_4 during the period of peak rainfall (Figure 1) when soils were at their wettest (Figure 2).

The gallery forest soil consistently had higher CH_4 oxidation rates than the other ecosystems and none of the four sampling areas were ever a source of CH_4. Low bulk density (Figure 3A), high water infiltration rates (Figure 3C), high air permeabilities (Figure 3I) and low resistance to penetration (Figure 3J) are physical attributes of soil in the gallery forest that explain these results. In contrast, all other land uses on the clay loam soil have lower values than the gallery forest soil for air permeability and hydraulic conductivity through the 30 cm sampling depth. The clay loam savanna and pasture soils showed the most physical constraints to drainage and gas transport in the top 10cm of soil, consistent with these two systems becoming a source of CH_4 during the wet season. The pasture soil had the highest water filled pore space (Figure 2B) and the highest CH_4 emissions of all systems during the month of July. Converting the clay loam savanna into cropland, reduced CH_4 oxidation rates during the dry season (Figure 4A and B), probably as a result of reduced availability of water. On the other hand, tillage improved drainage and aeration, reducing the length of time that agricultural soils become anaerobic, which results in only small emissions from these soils in the wet season.

Soil texture was an important factor affecting CH_4 fluxes in the two savanna sites. Methane oxidation rate in the sandy savanna soil was lower than that in the clay loam savanna during the dry season, probably because low water retention (Figure 2) reduced the population and/or activity of CH_4-oxidizing bacteria (Boekx et al., 1997; Bottner 1985) relative to the clay loam savanna soil. The greater total porosity, and especially macro-porosity (Figure 3F and 3G), favored the prevalence of aerobic conditions in the sandy savanna soil, which was never a substantial source of CH_4.
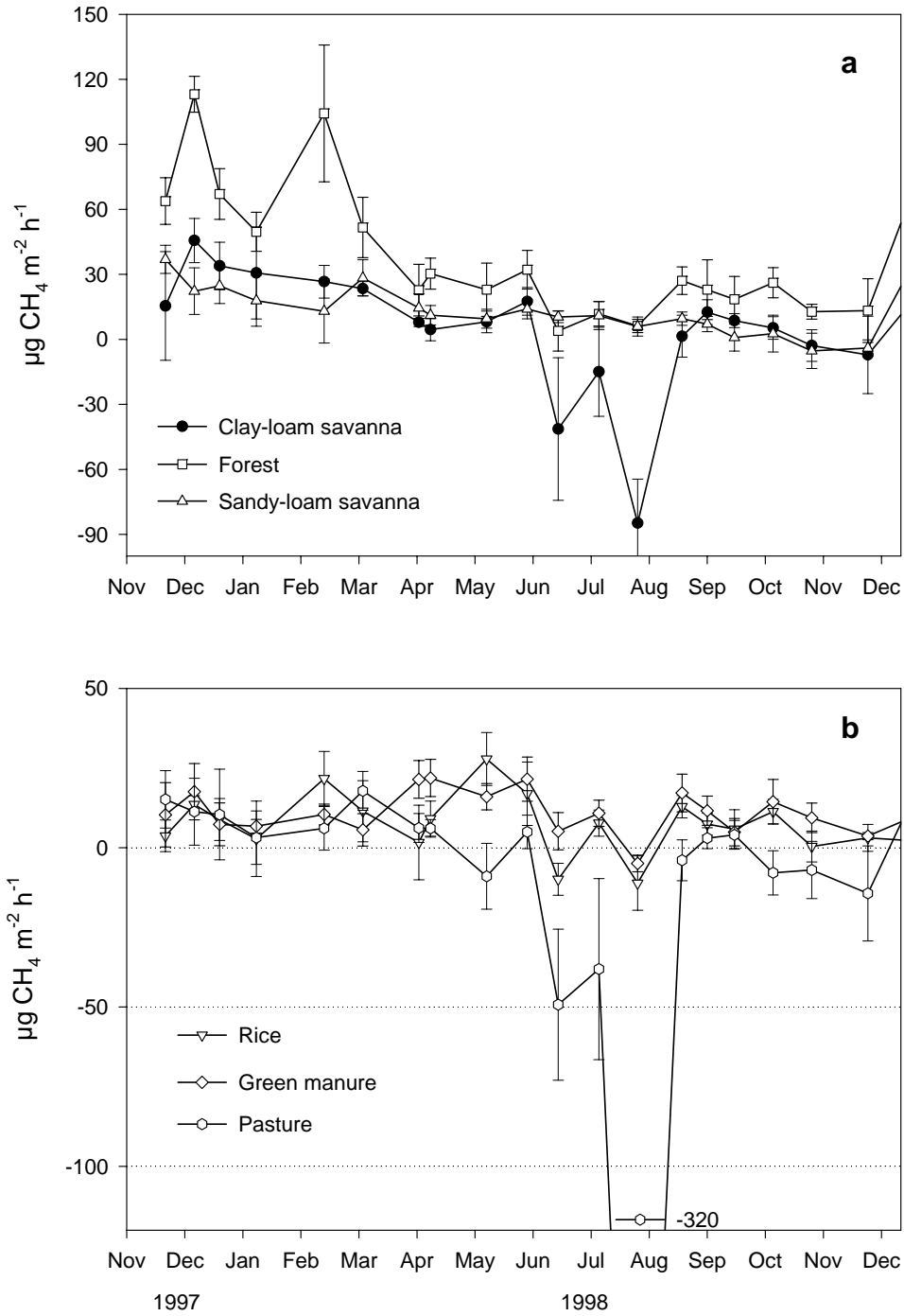
Figure 4. Land use effect on methane oxidation by soils in Colombian savannas. Positive numbers indicate net methane consumption by the soil (net sink)

Estimates of annual CH_4 fluxes are presented in Figure 5A. The gallery forest soil, with a sink strength of 3.05 kg CH_4 ha^{-1}y^{-1}, constituted the highest sink for CH_4. The CH_4 sink strength in the gallery forest is similar to values reported for a wet forest in Puerto Rico (Steudler et al., 1991), and other types of tropical forest in Central and South America (Keller, 1994; Keller and Reiners, 1994; Keller and Wofsy,

1986). The annual CH_4 sink strengths in the sandy and clay loam savanna soils were only about one-third and one-twelfth of that of the gallery forest soil, respectively. Methane sink strength in the Llanos clay-loam savanna soil (0.26 kg CH_4 ha^{-1}y^{-1}) is similar to values reported for grasslands on Oxisols of Puerto Rico (Mosier and Delgado, 1997), and higher than values reported by Sanhueza et al. (1995) for comparable savannas in Venezuela, which were found to be a minor source of CH_4. However, methane sink strength on well aerated, high clay Oxisols of the Brazilian savanna (Cerrados) was 1 to 2 times higher than that of the Llanos savannas (Lauren et al., 1995).
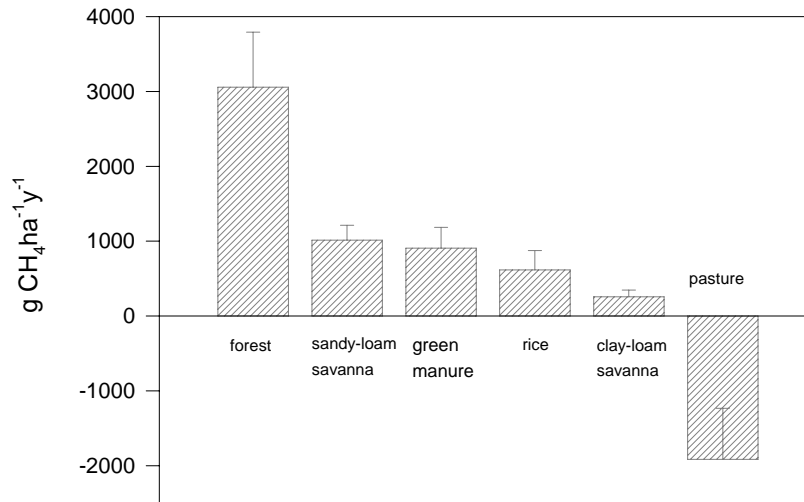

Figure 5. Annual methane oxidation by soils in Colombia savannas

Conversion of clay loam savanna to cropland increased CH_4 sink strength by 2.5x to x kg CH_4 ha^{-1}y^{-1} for rice mono-cropping and by 4x to y kg CH_4 ha^{-1}y^{-1}for the rice-cowpea rotation These results contrast with several reports (Sitaula et al., 1995; Mosier et al., 1991, Bronson and Mosier, 1994) showing a decrease in methane consumption rate when soils were fertilized with ammonium fertilizer sources. (However, information to specifically address effects of N status/source (fertilizer or green manure) on CH_4 oxidation capacity was not collected in the present study. Presumably, removal of physical constraints to gas exchange counteracted any negative effect of fertilizer on CH_4 oxidation rate.

Conversion of clay loam savanna to pasture changed the soil from a net sink to a net source (1.92 kg CH_4 ha^{-1}y^{-1}) of CH_4. A similar result was found for conversion of tropical forest in Costa Rica to pasture (Keller, 1983). Several other pastures sites in temperate (Van der Pohl, 1999) and tropical regions (Mosier and Delgado, 1997) have been found to be net sources of atmospheric CH_4. Keller and Reiners (1994) found that the condition of pastures greatly affected CH_4 emissions, with emissions from abandoned, degraded pastures being nearly five times higher than from pastures in good condition. The pasture plots used in the present study were 7-years old, originally planted with *B. dictyoneura* and *A. pintoi*, and supporting a stocking rate of 3 head/ha. Signs of pasture degradation were evident at time of sampling: low persistence of the legume, increased bulk density, subsurface compaction, reduced air permeability, occurrence of isolated termite mounds etc. Options are available to improve the management of these pastures in ways that reduce soil compaction and prevent or slow pasture degradation (Amezquita, 1998).

Nitrous Oxide

Fluxes of N_2O from soils of the native and agricultural systems over the one-year study period are shown in Figures 6a and 6b, respectively. Spatial variability in N_2O emissions was higher than that for CH_4, with RSD values mostly in the range of 100 to 200%, although values as high as 400% were

sometimes found. This level of variability is similar to that found in other studies (Williams et al., 1999; Ruser et al., 1998; Veldkamp et al., 1998; Keller and Reiners, 1994).
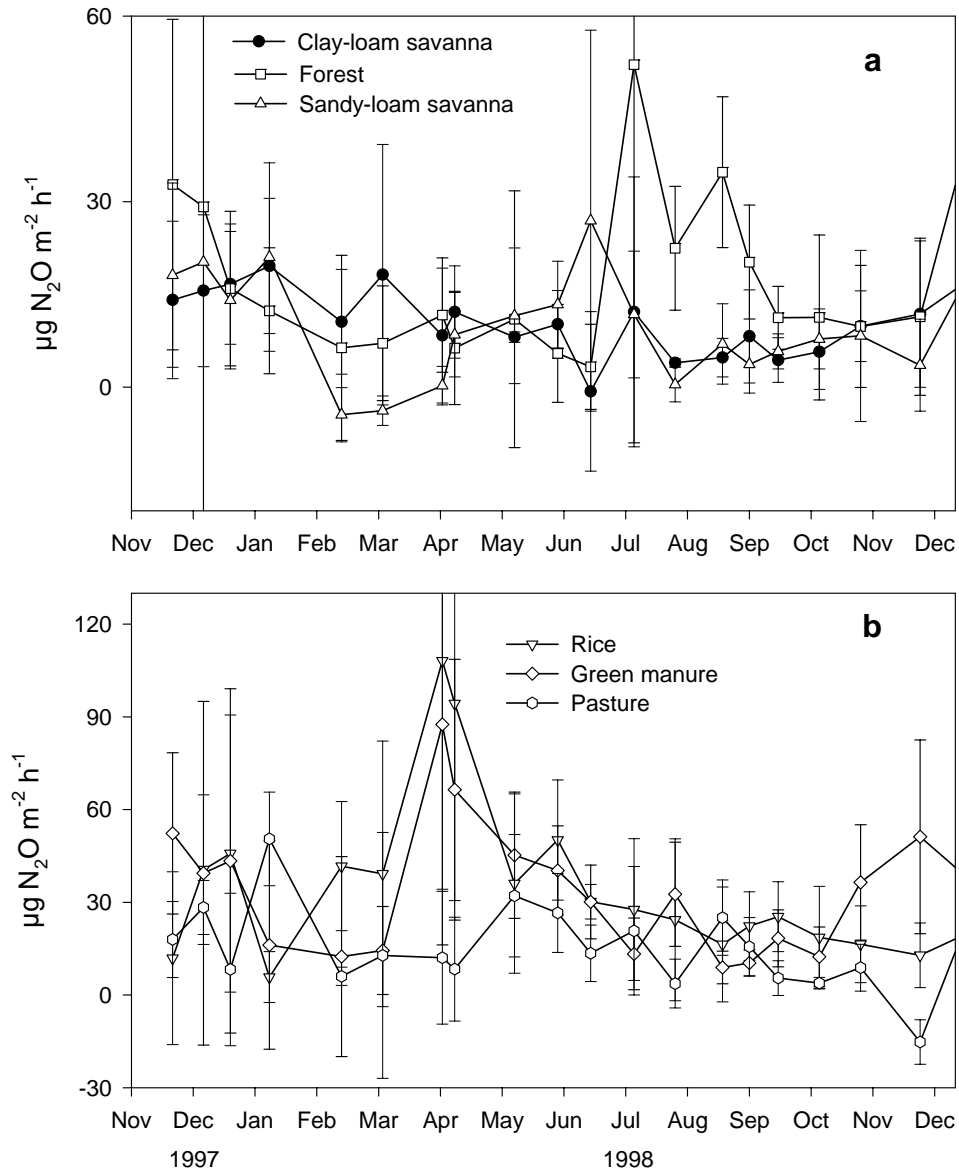

Figure 6. Land use effect on emission of nitrous oxide from soils in Colombian savannas

Soils of all land-uses were net sources of N_2O for most of the year, although small sink strengths occurred in the sandy soil savanna at the end of the dry season and in the pasture soil at the end of the rains. Emission rates from natural ecosystem soils were generally low, with the gallery forest the main contributor. A peak of emissions was approximately coincident with the peak of the rainy season in the gallery forest. No consistent difference was found between the savannas on soils of contrasting texture. Observed low emission rates in native land uses may be partially the result of the small amount of nitrogen that is cycled in these nutrient-limited soils (Figure 7) and low soil pH, which reduces both nitrification and denitrification rates (Broadbent et al., 1965; Jackson, 1967).

The increase in external nitrogen inputs and cycling increased N_2O emissions in all of the agricultural systems compared to the clay loam savanna. Biological N fixation contributes to the improved productivity of the grass-legume pasture (Thomas et al., 1997), and the cowpea green manure is estimated to supply 100-120 kg N $ha^{-1}y^{-1}$ in the rice-cowpea rotation (Friesen et al., 1997). The mono-crop rice received 80 kg N $ha^{-1}y^{-1}$. Enhanced nitrogen cycling in the pasture is due also in part to nitrogen return via urine and dung from the cattle. Yamulki et al (1998), estimated that 7% of urine-N is lost as N_2O. Both tillage and fertilization/green manuring contribute to increased nitrogen levels in cropped soils. The highest emissions of N_2O in the cropped systems were observed in April, coincident with N additions and high soil nitrate levels (Figure 7).
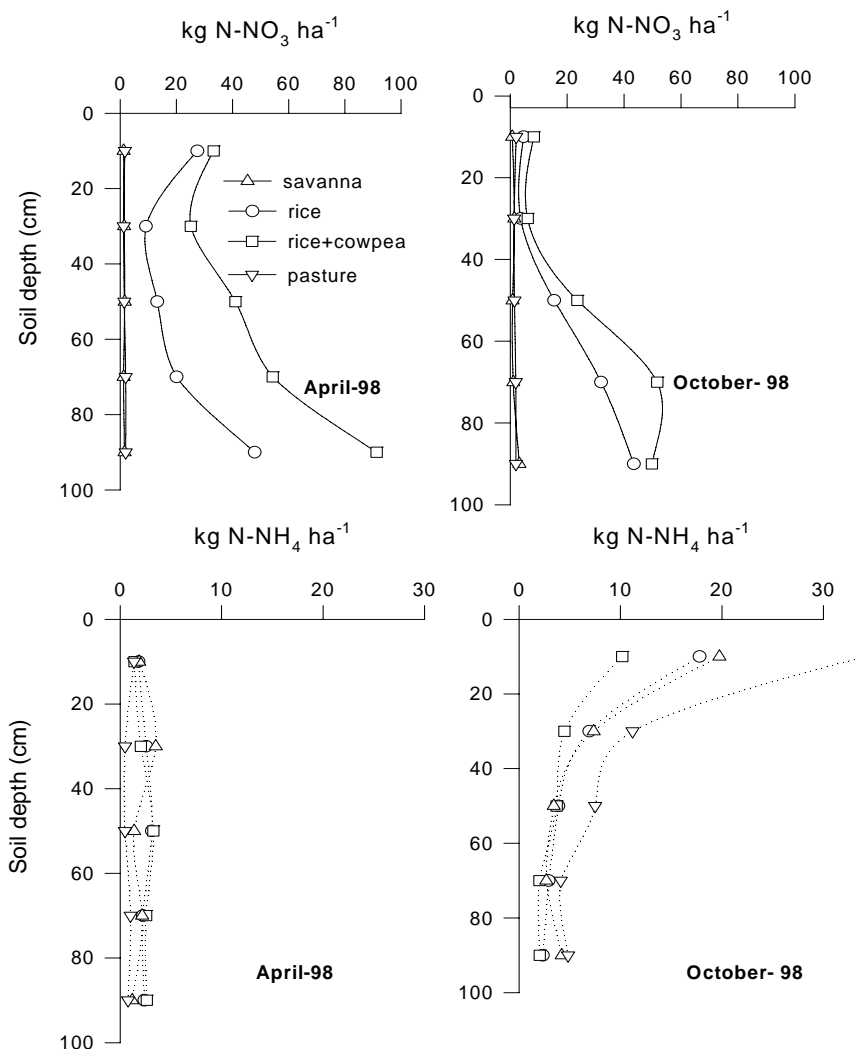

Figure 7. Nitrate and ammonium levels in the soil profile

Integrated annual net fluxes of N_2O are summarized in Figure 8. All land uses were a net source of N_2O. Within the natural ecosystems, the annual emissions from the gallery forest (1.44 kg N_2O $ha^{-1}y^{-1}$), were significantly higher than those from the clay-loam savanna (0.94 kg N_2O $ha^{-1}y^{-1}$; $p<0.01$) and the sandy savanna (0.76 kg N_2O $ha^{-1}y^{-1}$; $p<0.05$). The annual emission of N_2O from the gallery forest is low (HOW LOW??) compared to rainforest in Central America (Keller, 1994), similar to estimates for the forests in the Amazon (Culman, 1995) and eastern Venezuela (Sanhueza et al., 1990), and higher than values for semi-deciduous dry forest in Mexico (Davidson et al., 1993).
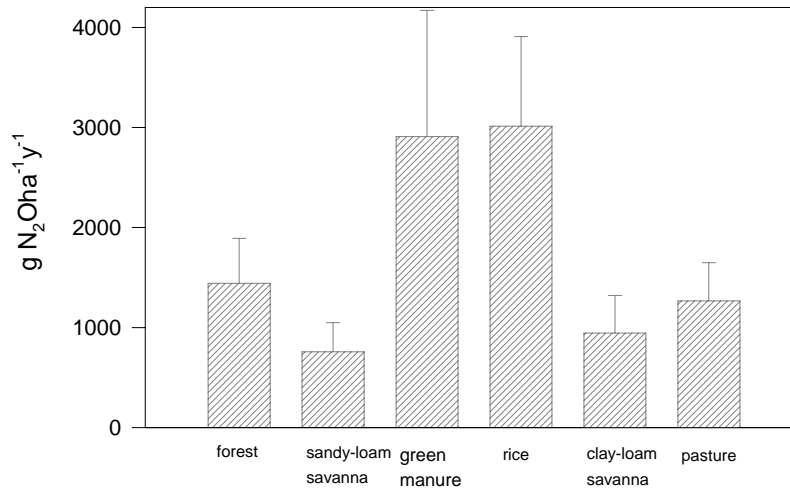
Figure 8. Annual nitrous oxide emission from soils in Colombia savannas

Emission rates for the savannas are similar to those reported for the Brazilian Cerrados (Nobre, 1995; Lauren et al., 1995) and for native grassland bordering the Guyana rain forest in Venezuela (Sanhueza et al., 1990), but were higher than those reported for the more comparable savannas of Venezuela (Hao et al., 1988).

Conversion of clay loam savanna to a grass-legume pasture did not significantly increase N_2O emissions although legumes are known to do this (Galbally et al., 1992; Duxbury et al., 1982). A possible reason is the relatively low proportion of legume in the pasture studied. The annual emission value of 1.27 kg is lower than values for temperate grasslands (Williams, 1999; Ball et al., 1997a; Van den Pohl, 1999) or from fertilized pastures in Costa Rica (Veldkamp et al., 1997), but falls within the range found for degraded pastures in Costa Rica (Keller and Reiners, 1994), and Puerto Rico (Mosier and Delgado, 1997).

Annual emissions of N_2O were significantly increased ($p < 0.01$) by slightly more than three-fold when clay loam savanna was converted to cropland. There was no difference in emissions between the two rice systems (Figure 8), where N is supplied predominantly through inorganic fertilizer in the monocrop and via organic sources in the rotation. This result does not support the suggestion (Freney, 1997), that more N_2O is emitted from organic than inorganic N sources. The observed emission rates in the rice systems of 2.8-3.0 kg N_2O $ha^{-1}y^{-1}$ correspond to 1.8% of external nitrogen inputs after removing the contribution of the background flux from the savanna soil. This proportion is higher than the value of 1.25% x fertilizer-N which has been frequently used as an average for fertilized fields (Mosier et al., 1995), but lower than the more recently suggested proportion of 1.25% x fertilizer-N + 1 (Hopkins et al., 1997). The data is similar to other studies on tropical acid Oxisols (Mosier et al., 1998), where the conversion of the native ecosystem to agriculture, with additions of 100kg N as fertilizer, resulted in a five-fold increase in N_2O emissions from soil.

Budgets for Soil Sources of Methane and Nitrous Oxide in the Llanos

The Radiative Forcing Potential of the Llanos

The role of the soil

Table 1 shows figures for the area of the various land uses found in the Llanos, as well as their estimated contribution to annual net fluxes of methane and nitrous oxide. Data for coverage area corresponds to the nearly 14 Mha of the so called well-drained savanna which is more suitable for intensification of agriculture or pastures (Rivas, 2000).

By contributing about half of the total methane sink, soil in the gallery forest plays a key role in the net balances of this trace gas in soils of the Llanos. Given the relatively small area covered with forest, any disruption could have an important impact on regional soil methane sink strength. To illustrate this, if current forest area were reduced by 50%, the net methane sink by soils from the Llanos would be also reduced by 50%. Crops included in this study are not the only ones currently used or likely to be used in the future, and therefore a degree of uncertainty arises in regional gas budgets when it is assumed (as in Table 1) that rice as a monocrop and in rotation with green manure are representative of the effect of cropland in the region. However, given that the area under crops is still small, their potential contribution to changes in balances of methane in the Llanos is probably not too high, even under the scenario of a two fold increase in cropland expected for the next two decades (Smith at al., 1997). The annual sink strength of methane in soils from the Llanos (0.0078 Tg/y) represents around 0.02% of the estimated 40 Tg/y global soil sink strength (Minami, 1997).

Total N_2O emissions are greatly controlled by the native land uses (savannas and gallery forest), due to their high area coverage. Crops and pastures contribute currently in similar proportions to the overall budget of this gas in the Llanos. The global annual emission is low (0.1%) with respect to the estimated global planetary emissions of 13Tg/y (Bowman, 1994).

Table 1 Contribution of land uses to the budgets of CH_4 and N_2O from soils in the Llanos

Land Use	% of the area	Area x10^6 ha	CH_4 oxidation rate g ha^{-1}y^{-1} (^)	Annual CH_4 oxidation Mg	N_2O emisión rate g ha^{-1}y^{-1}	Annual N_2O emission ton	% of total CH_4 sinks	% of total N_2O sources
Silty-Clay savanna	69	9.5	256 (90) b	2432	944 (375) ab	8968	27	61
Sandy savanna	13	1.8	1014 (199) c	1825	758 (291) a	1364	20	9
Gallery forest	10	1.4	3057 (736) a	4280	1442 (449) b	2019	48	14
Cropland (*)	4	0.5	762 (267) c	381	2961 (1079) c	1481	4	10
Pasture	5	0.6	-1915 (683) d	-1149	1266 (382) b	760	-	5
Llanos total	100	13.8	532 (201)	7769	1032 (389)	14591		

(*)Average of the values found for rice monocrop sites and cowpea - rice rotations. (^) Values in parenthesis are standard errors. In a column, values followed by the same letter indicate non-significant difference at p<0.05.

The contribution of termites

At least two types of termites are found in soils of the Llanos: subterranean soil-feeding termites and mound building termites (Decaëns, 1995). In a study conducted simultaneously with this, Rondón (2000) has shown that essentially all methane generated by subterranean termites is oxidized by soils before escaping into the atmosphere. The only contribution to net emissions of this gas is made by species of mound building termites of the genus Spinitermes. Annual estimated fluxes due to termites were reported as 6.7 and 7.2 g CH_4/ha for pastures of *B. humidicola* and native savanna respectively (Rondón, 2000). These values are fairly low compared to net soil sinks in the region, and consequently methane emissions by termites does not constitute an important component in the budgets of this gas in the Llanos. Soils under other land uses did not have termite mounds. To extrapolate annual fluxes of methane from termite mounds to the overall area of the Llanos covered with native savanna (in clay and sandy soils) and with pastures, it has been assumed that the density of 36 active mounds per hectare reported by Rondón (2000), for native savannas and 26 for pastures, applies throughout the Llanos. The integrated annual methane flux coming from termite mounds in the Llanos is 76 Mg CH_4/year. This value is only about 0.0004% of the total global emissions of 19.7 Tg CH_4 attributed to termites (Sanderson, 1996).

The "hot" effect of biomass burning

Towards the end of the dry season, vegetation in the savanna becomes too dry to be of value for cattle. To favor the re-growth of higher quality grasses, ranchers frequently burn their savannas. This, in addition to common natural fires results in a complete burning of the savannas at least every two years. Burning affects fluxes of GHG by two mechanisms: direct emission to the atmosphere in the form of the products of combustion, and indirect effects created by disturbances of the normal fluxes of gases from the soils. In a parallel study, Rondón (2000) measured both direct emissions of methane and nitrous oxide and long-term effects of burning on soil-atmosphere exchange. Extrapolating annual emissions to the area of the Llanos which is susceptible to burning (9.96 million hectares), direct emissions of methane due to burning were estimated to be 67,728 Mg CH_4/y, while indirect effects represent a reduction in 723 ton CH_4/y in the soil sink capacity (Rondón, 2000). The net annual release of methane by burning is then 68451 Mg per year, which is nearly 11 times higher than total methane oxidation by soils. Burning consequently has a major role in the annual budget of methane in the Llanos. The combined release of nitrous oxide in the region due to burning is 6928 Mg N_2O/year, which is about 37% of the total emissions of this gas by soils in the region. Its contribution is then also important though not dominant in the regional balance of nitrous oxide.

The "gaseous" role of cattle in the Llanos

Methane emission by cattle is a well-documented process, believed to be responsible for annual emissions on the order of 90 Tg (Johnson, 1996) or approximately half of total agricultural sources (Cole et al., 1997). Unfortunately there is a complete lack of data regarding methane emission by cattle grazing native savanna vegetation or improved pastures in the Llanos. Cattle population in the well drained Llanos is estimated to be around 2.5 million animals (Fedegan, 2000). Kurihara et al., (1999) reported methane emissions by cattle fed on tropical grasses of the order of 113g CH_4/cow-day. Though grasses are different, assuming the same methane production rate for cattle in the Llanos, the estimated production of methane by cattle in the region would be approximately 103,000 ton/year. This is about 16 times higher than the net sink by soils. This demonstrates the key role of cattle in controlling the budget of methane in the Llanos.

The total number of cattle in the Llanos is not expected to increase significantly in the near future due to market and demand constraints. What is expected with the introduction of improved pastures, is that cattle will move from native savannas frequently in remote locations, to improved pastures near to the roads and infrastructure. There are probably good opportunities to improve balances of methane in the region by offering better quality forage for the cattle. Future research in the Llanos should in consequence, try to account for the effect of improved diets on local methane budgets.

Balances of CH_4 and N_2O in the Llanos: four actors in the scene, just one landscape

In Table 2 results from the contribution of the major components of gaseous exchange are presented, and extrapolated to the respective area of influence to generate total annual fluxes for the Llanos. Data in Table 2 indicates that all together, the savanna ecosystem constitutes a net source of atmospheric methane, being largely controlled by direct emissions generated by burning and by the unfortunate 'bad breath" of cattle. The Llanos emits only about 0.03% of the total estimated global annual emissions of methane (535Tg, IPCC, 1997), and about 0.1% of total annual emissions of nitrous oxide. Covering an area of approximately 0.094% of the planetary land area, the region shows emissions of N_2O similar to planetary averages, while emission of CH_4 is only around one third of average global emissions. The Llanos can consequently be labeled as an environmentally friendly ecosystem. Despite that, there are opportunities to further reduce emissions of GHG's in the region.

Table 2   Net annual fluxes of CH_4 and N_2O in Colombian savannas

Contributing factor	CH_4 flux g ha^{-1}y^{-1}	N_2O flux g ha^{-1}y^{-1}	Total area affected Mha	Net CH_4 flux Mg y^{-1}	Net N_2O flux Mg y^{-1}
Flux from Soils (*)	-563	1,057	13.8	-7,769	14,591
Effect of burning on soil emissions	73	456	10	723	4,538
Direct emission in burning products	6,800	240	10	67,728	2,390
Emission by cattle (♣)	24,747	--	4	103,110	--
Termite mounds	7	0.008	11	76	0.1
Total in the Llanos			13.8	163,868	21,519
Total flux in the Llanos (Tg/y) (^)				0.164	0.021

(*) Value was calculated as the weighed average of fluxes and areas under various land uses in the region (Table 1).
(♣) An average stocking rate of 0.6 heads/ha was assumed for the Llanos (Rivas, 2000)
(^)Termite mounds were considered for the soils under savannas and pastures.

Mitigation strategies

Data in Table 2 indicates that mitigation strategies should be directed towards reducing the frequency of fires and reducing emissions by ruminants. Probably there is a little opportunity to favorably alter emission factors by burning at other times during the dry season, this impact has to be evaluated. Burning is however very important for maintaining the productivity and functioning of the ecosystem and also to permit the current economic exploitation of the savannas.

Therefore, unless more profitable management options are offered to farmers, there is little opportunity to reduce the scope of fires in the savannas. Pastures could play a role here, as they are economically feasible options for the development of the region (Vera, 1997). As was mentioned before, improved pastures with mixtures of high productivity grasses and forage legumes could also play a role in reducing emissions of methane by animals in the region.

In Table 3, the combined effect of all components on the balances of methane and nitrous oxide has been integrated to provide annual emissions per unit area in each land use. Though pasture soils were found to be a net source of methane, the fact that burning is eliminated in well managed pastures counteracts emissions by soil. However, given that stocking rate is increased six fold when converting a unit area of savannas into pastures, there is a 4.6 fold increase in the net release of methane to the atmosphere per unit area due to the cattle. Taking all the factors into consideration, conversion of savannas to cropland is the only alternative identified in this study, which can convert the savanna ecosystem into a net sink of methane, by eliminating the sources (burning and termites) and enhancing the soil sink. This option would however increase net emissions of nitrous oxide and consequently a "compromise solution" should be adopted when trying to include the environmental perspective within the development programs for the Llanos. It is clear however, that under the low fertilizer application rates expected to be used in the Llanos, crops will provide a good alternative to the development of the region in an "environmentally friendly way".

Clearly, regenerating forest on deforested land will provide the best alternative to mitigate emission of greenhouse gases in the Llanos. Unfortunately this is not an option easy to implement, because fire normally prevents the advance of forest into the savanna. This implies that measures to prevent the fire from reaching the borders of the forest should be reinforced, but that normally involves high cost in building roads which the farmers will not be able to afford if they are only for the sake of the environmental benefit. One possibility to cope with this problem would be to foster the use of areas near

the borders of the forest as pastures or croplands. It is however reasonably to expect that governmental subsidies should be employed to make this option feasible. Perhaps there is an opportunity to recruit some funds by selling the equivalent GHG offset resulting from recovering forest (Moffat, 1997).

Table 3. Annual integrated emission of CH_4 and N_2O per hectare in various land uses in the Llanos.

	Savanna	Sandy savanna	Gallery forest	Pastures	Crops
CH_4	27.3	26.5	-3.1	125.7	-0.8
N_2O	1.6	1.5	1.4	1.3	3.0

Values are in kg $ha^{-1}y^{-1}$ (Negative values indicate a net sink)

Soil carbon, a solid component in the greenhouse gas analysis

Soils of the Llanos have been found to be able to sequester important amounts of atmospheric carbon when deep rooted grasses are introduced in these lands. Net C sequestration by pastures of *Brachiaria humidicola* in the top 1m deep soil was reported as 25.9 ton C in a ten year period, while grass-legume pastures of *B. humidicola* and the forage legume *Arachis pintoi* increased such amounts to 70.4 ton/10 years (Fisher et al., 1994). Though in this study fluxes of CO_2 were not considered, It is clear that the extent of the reported carbon accumulation in soils under pastures plays a main role in configuring the complete scenario of GHG's in the Llanos. Consequently, an analysis will be attempted here to include this component.

The radiative forcing strength of the Llanos

As a mechanism for integrating the combined effect of all greenhouse gases involved in the Llanos, the CO_2-equivalent global warming potential (E-GWP) of CO_2, CH_4 and N_2O has been calculated for two time horizon scenarios (20 and 100 years), for every land use in the Llanos. In a 20-year time scenario, CH_4 has a GWP equivalent to 62 times that of CO_2, while that of N_2O is 275 times compared to CO_2. In the 100 years time horizon, the corresponding GWP values for CH_4 and N_2O are respectively 23 and 296 times that of CO_2 (IPCC, 2001). The calculation of integrated E-GWP expressed as equivalent kg of CO_2, was done by multiplying the per hectare annual emission of CO_2, CH_4 and N_2O from each contributing factor, by the land area associated with that factor and then by the relative GWP of each gas. Adding together the values obtained for each factor gives the overall equivalent E-GWP for the Llanos, expressed as equivalent units of CO_2. For the calculation, it was assumed that burning does not make a net contribution to emissions of CO_2, because the CO2 released by fire is reabsorbed from atmosphere during vegetation regrowth. Stocking rate of cattle was assumed as 0.5 head/ha in clay and sandy savannas and 3 head/ha in pastures. The same CH_4 emission factor for cattle was used for improved pastures and for native savannas. Soil emissions of CH_4 and N_2O were assumed to be the same in grass alone and in grass-legume pastures. Figure 9 shows calculated E-GWP values (for one year total emissions of all GHG's) on a hectare basis for the various land uses and has been calculated for two time horizons, 20 and 100 years of influence. Figure 9 includes the reported (Fisher et al., 1994) values for carbon sequestration in pastures of grass-legume (0.1Mha) with a high rate of carbon sequestration (70.4 ton C/ha in a 10-year period), as well as pastures of grass alone (0.5Mha) with lower rate of carbon accumulation (25.6 ton C/ha in a 10-year period). Annual carbon sequestration by pastures was calculated assuming the same rate of accumulation for each year, and then converting it into CO_2.

All natural land uses (savannas and forests) show positive equivalent E-GWP values, indicating that they are contributing to the radiative forcing of the atmosphere. The gallery forest is clearly the best natural land use from the perspective of the heating effect on the atmosphere. Its equivalent E-GWP is very low in both time scenarios. At the 20-year horizon, the warming contribution from the gases emitted during one year by one hectare of forest is equivalent to that of the CO_2 emitted by the combustion of 35 gallons of gasoline (fuel for 8 hours trip of a small car!). Including all the sources and sinks, the radiative

power of savannas is low and decreases when the 100 year time scenario is used, because most of the contribution is in the form of CH_4, which is a short lived gas in the atmosphere. Crops have integrated E-GWP lower than that of the savannas in the 20 year scenario and approximately the same as the savannas in the 100 year scenario. The conversion of savanna land into cropland does not have a detrimental effect on the E-GWP.
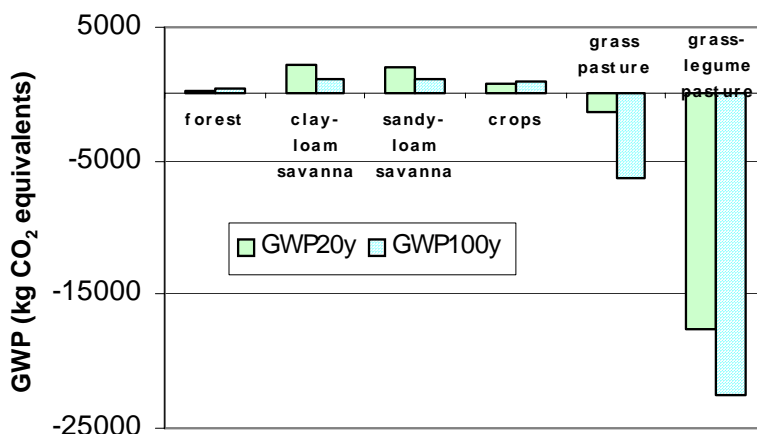

Figure 9. Global warming potential –GWP for various land uses in the llanos under two time horizons scenarios (20 and 100 years). GWP is expreed as kg of CO_2 equivalents. Values represent the contribution of annual emissions per hectare.

The inclusion of pastures in the Llanos plays a much more important role in affecting the overall E-GWP. Due to the modest emissions of methane and nitrous oxide from pastures and the very high sequestration of atmospheric CO_2 as soil organic carbon, pastures can convert the system from a modest source into an important net sink of radiatively important species. The rate and persistence of C accumulation plays a major role in the strength of the sink, especially in the 20-year horizon. Even with rates of C accumulation in soil of around half of the reported value for grass alone pastures in Carimagua, the equivalent E-GWP of annual emissions from one hectare of pastures would be zero.

The Llanos in the year 2020
Land use patterns in the Llanos are expected to change in the next two decades. Studies suggest (Smith et al., 1997; Rivas, 1999), that the area of crops could increase up to two times the current values while the area under pastures will also double in the same period. The area under grass-legume pastures is expected to grow from 0.1 to 0.3 Mha, while the area under grass alone pasture will continue to dominate and will increase from 0.5 to 0.9 Mha. This expansion will be at the expenses of the clay-loam savanna, which has slightly better levels of soil nutrients than the sandy savanna. The area under gallery forest will probably decrease by 10% in the next 20 years assuming the same rate of current intervention. Annual rate of C-sequestration by pastures in soil was assumed as reported for grass alone and grass-legume pastures at Carimagua (Fisher et al., 1994).
Table 4 shows results of a calculation of the integrated E-GWP for the Llanos at present and in the year 2020 for a 20-year time horizon. Under current land use distribution, the Llanos as a whole plays a minor role in the radiative forcing in the earth's atmosphere. Its integrated E-GWP of 9.6 Tg of CO_2 equivalents is only about 0.004% of estimated global planetary radiative contribution of about 242,000 Tg of CO_2 equivalents (IPCC, 2001).

Table 4. Integrated E-GWP for the Llanos under present and expected land use distribution in the year 2020. Values are equivalent Tg of CO_2 calculated for a 20-year time horizon.

Land use	E-GWP kg CO_2 equivalents per ha	Area (Mha)		Integrated E-GWP (Tg of CO_2 equivalents)	
		present	Year 2020	present	Year 2020
Forest	207	1.4	1.26	0.29	0.26
Savanna	2140	9.5	8.54	20.33	18.28
Sandy savanna	2042	1.8	1.8	3.68	3.68
Croplands	767	0.5	1.0	0.38	0.77
Grass alone pasture	-1358	0.5	0.9	-0.68	-1.22
Grass-legume pasture	-17674	0.1	0.3	-1.76	-5.30
Total				22.24	16.46

In Figure 10, in addition to the 20-year time horizon a longer term 100-year time horizon has been used to calculate effects of present and expected land use distribution in the Llanos. The development of the Llanos will have small net benefits to the environment by reducing the radiative force of the atmosphere. This benefit will be accentuated in the longer term scenario. Once more the minor role of the Llanos in the context of warming of the planet is emphasized.

Figure 10. Integrated GWP for the Llanos under present land use and expected land distribution in the next two decades. Two time horizons (20 and 100 years) are considered.

Conclusions

This study presents the first data set on fluxes of methane and nitrous oxide for the Colombian Llanos. Results indicate that gallery forest is an important sink for atmospheric methane, while savannas are a minor sink. Therefore, preservation of the gallery forest should be of priority concern as this environment also provides a home for a large biodiversity of endemic plants and animals.

Conversion of soils into cropland does not reduce their methane oxidizing capacity and some of the management practices could even increase their sink strength. This may be the result of eliminating some of the physical constraints that limit the gas exchange between soil and the atmosphere (soil compaction, surface sealing etc.). On the other hand it also increases emissions of nitrous oxide and is equally expected to increase losses of soil carbon as a result of tillage. Despite this, given that the main contributing factors (burning and cattle) are excluded in cropland, it can be anticipated that agriculture will be a better option than savanna for reducing the radiative forcing of the Llanos.

Emission of methane by biomass burning is a key factor in the balance of this gas in the Llanos. Any action that can reduce the area submitted to burning and or the frequency of burning events, will improve the radiative balance in the region. In this respect, conversion of savanna into croplands or pastures is clearly an advantage because burning is eliminated in such land uses. Promoting the re-colonization of the land by gallery forests constitute a win-win situation as it will not only eliminate the burning, but also will increase the methane soil sink strength.

Fire plays a key role in maintaining the biodiversity in the savanna, in addition to other important though not fully understood ecological roles. Consequently, complete suppression of the burning is not a desirable option. Appropriate corridors to maintain the continuity of the savanna ecosystem should always be considered.

Cattle-associated emissions of methane dominate methane budgets in the Llanos. Improving estimates of their actual contribution as well as exploring promising opportunities to reduce their impact by offering forages of higher nutritional value, are important topics for research in the near future.

Natural ecosystems as well as converted lands constitute small net sinks for N_2O in the Llanos. Emission rates are related with the amounts of nitrogen cycled in the soil; nitrogen inputs in the form of fertilizer or green manure cause enhanced emissions. Strategies to manage these inputs in order to minimize nutrient losses and reduce environmental impact require further attention.

In general fluxes of methane and nitrous oxide from soils in the Llanos can be considered low, but fall within the range reported for similar environments in Africa (Seiler et al., 1984), Central America (Mosier et al., 1998), Brazil (Lauren et al., 1995) and Venezuela (Scharffe et al., 1980), and even for tall grass prairies in temperate regions (Tate and Striegl, 1993).

Though pastures will increase methane emissions from cattle due to the increase in the stocking rate as compared to savanna, by avoiding the fire and by sequestering atmospheric CO_2 in the form of soil organic carbon, pasture is the only land use option identified in this study, that can shift the land from a net source into a net sink of atmospheric GHG's.

Influencing the direction of change

This study has shown that the Llanos are only a very minor contributor to the warming of the atmosphere and that expected intensification of agriculture and cattle production in the coming two decades would not have negative effects on the radiative forcing potential of the region. Despite this, there are other well identified constraints for the sustainability of the natural resource base, whose impact should never be forgotten. Pasture degradation is major cause of pasture abandonment specially in the Brazilian Cerrados and the Amazon. Degradation could result not only in reduced C sequestration in soils but even turn them into net sources of Carbon (Da Silva et al., 2000). Though current pasture degradation is not too severe in the Llanos, unless appropriate management practices were adopted, this could become a critical problem in the region, whose environmental consequences are still to be evaluated.

In the jargon of optometrics, 20-20 means perfect vision. We hope that appropriate vision will be used by policy makers in the design of development plans for the Llanos which allows the region to continue being an environmentally friendly ecosystem in the year 2020.

Acknowledgements

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Carbon Storage in Soils from Degraded Pastures and Agroforestry Systems in Central Amazônia: The role of charcoal

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Introduction

The vicious cycle of deforestation: Vast areas of the Amazon rainforest have been cleared in the last decades to be converted into pastures. After few years of use, the land is degraded as a result of nutrient depletion, soil compaction and surface sealing. Productivity declines severely and pastures become abandoned, giving place for a succession to secondary forest. A new forest area is then usually cleared to start the process again. Abandoned lands are characterized by very low storage of nutrients and reduced stocks of soil organic carbon (SOC). Some alternatives do exist to recuperate degraded land including the establishment of agroforestry systems. These options are expected to help in restoring soil nutrients and allow C sequestration in both biomass and soils. This poster presents information on C storage in soils under 10 year old agroforestry systems and secondary vegetation, as well as on primary forest for an area in the Central Amazon.

The Charcoal contribution. Natural and anthropogenic fires are frequent in the Amazon forest. Combustion of plant material is never complete specially for roots, and this result in variable amounts of residual charcoal being added to the soils. Charcoal is ubiquitous in Amazonian soils and is present in a range of size particles: from coarse (>2 mm diameter) usually found mostly at the soil top layers, to very fine particles (<50 µm) distributed along the soil profile.

Charcoal is mainly carbon in an extremely inert form but until now not much effort has being devoted to define this as a separate C pool in soils. Given its inherently heterogeneous distribution, charcoal presence creates problems when trying to assess the effect of a given land management option on C sequestration by soils. Changes of SOC are normally small for short to medium terms and could be masked by the "noise signal" created by the charcoal. This noise also confounds interpretation of the dynamics of SOC when the ^{13}C technique is used (Desjardins et al., 1996). To be able to separate any difference in SOC resulting from different land use, charcoal contribution to total soil C has to be assessed. In this study we evaluated the contribution of different charcoal size classes to total soil C.

Materials and Methods

The project is being conducted at EMBRAPA-CPAA research station at km 54 north of Manaus, Brazil. In a long-term experiment, four alternatives to recover degraded land in the Central Amazon have been studied: establishment of two silvopastoral (SPS) and two agroforestry (AFS) systems: SPS included ASP1 (medium fertilizer inputs) combining *Brachiaria brizantha*, *Desmodium ovalifolium* and mahogany (*Sweithenia macrophyla*) and low input ASP2 in which *B. Brizantha* has been replaced by *B. humidicola*. AFS were: AS1 based on palm species(*Bactris gasipaes and Euterpe olearaceae*) and also includes Cupuaçu (*Theobroma grandiflorum and Colubrina acreanaea*). AS2 is based in native and exotic fruit trees (6 species) and also includes Mahogany and Brazil nut (*Bertholletia excelsa*). Secondary vegetation of similar age to the AFS and primary forest soils have been used as controls. Three repetitions of every

system and control were evaluated. The area has a mean annual rainfall of 2250 mm and average temperature of 28°C. Soils are high clay Oxisols, very low in fertility.

Given the complexity of the AFS studied, to obtain a representative sample of soil from a given systems is a complex task. Soil sampling was based on a species-interaction strategy. In each plot (3000 m^2), a composite soil sample of five sites was taken from each of the main plant-plant interaction found in the plot. Samples were separated at 0-5, 5-15, 15-30, 30-60 and 60-100 cm depth. Soil was air dried and gently dissagretated to <4mm diameter. A type Jones sample divider was used to separate soil in three size classes: 2-4 mm, 0,5-2mm and less than 0,5 mm diameter. Charcoal was separated by hand in a subsample of the 2-4 mm (G) and 0.5–2mm (M) size. Then, the original sample (free from medium to large size charcoal) was reconstituted to be analyzed for total C and nutrients. In a subset of samples, the fine fraction was used to determine black carbon content using the methodology of Kuhlbusch (1995). Finely ground soil (<53 um) was oxidized with repeated doses of NaOH (four times), HCl, HNO$_3$, H$_2$O$_2$, H$_2$O and finally thermally oxidized in a Oxygen-rich environment at 350C for 3 hours. C content in the original sample and the final residue were determined in a dry combustion CHN analyzer. C content in the residual soil after the chemical and thermal oxidation is defined as black carbon, and in addition to charcoal it includes the most highly resistant components of SOM.

Results and Discussion

Charcoal. Figure 1 shows the relative contribution from charcoal in each size class to total charcoal for the case of the ASP1 system. Charcoal in medium and large sizes is more abundant in the surface and subsurface layers and decays strongly as soil gets deeper. It is worth nothing however, that medium size particles are found even at 1m depth suggesting or localized burning of deep roots or migration of charcoal from the surface probably through root or soil fauna channels. Variability in charcoal content in the M and G size classes was high indicating non-homogeneous distribution of charcoal in soils. The contribution of the fine fraction is much more homogeneously distributed through the soil profile.
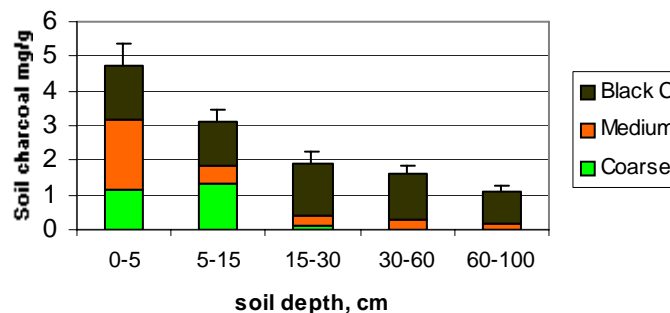

Figure 1. Charcoal distribution in various soil particles sizes. System ASP1.

Figure 2 represents the relative contribution of charcoal fractions to total soil C. It can be seen that charcoal can account for between 5 and 15% of total soil C, with higher proportions found in the top soil layers.
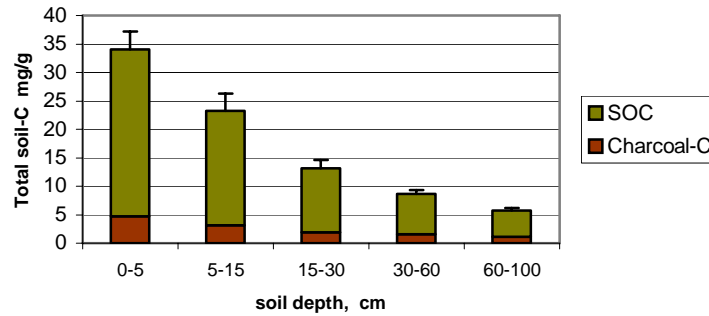
Figure 2. Charcoal contribution to total soil-C. System ASP1.

Soil C stocks. There were found significant differences among C stocks in most soil layers except in the surface layer where variability was the highest. Figure 3 shows the C stocks stored in the 60-100 cm depth soil layer. Carbon storage at that layer was higher in the primary forest soil as compared to other systems, being followed by the fruit based system (which includes some large trees), suggesting an important contribution from deep roots to C buildup. The ASP2 low input system presented the lowest C storage at such depth. This is in agreement with lower aerial biomass estimates for such system reported by McCaffery (Poster in this meeting).
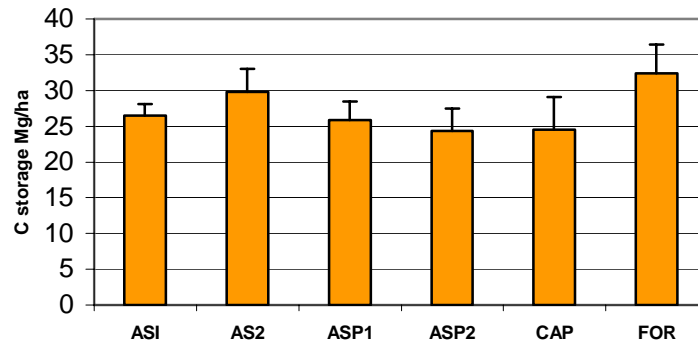

Figure 3. C storage in soils at 60-100 cm depth

In Figure 4, total C storage in the soil profile is presented for all systems (data correspond to C content after removing the coarse and medium size charcoal fragments). Significant differences were found between systems. When the charcoal contribution is taken into account, such differences become hidden. Forest soils store the highest amount of C (121 Mg.ha^{-1}), followed by the AS2 system with 116 Mg.ha^{-1}. On the other extreme, soils under secondary vegetation and ASP2 system presented the lowest stock (106 Mg.ha^{-1}). Results in this study indicate that agroforestry systems permit a moderate recovery of soil C stock relative to the control under secondary vegetation. Rates of C accrual are in the order of 1.8 Mg.ha^{-1}.y^{-1}. This contrasts with much higher rates reported for temperate and tropical regions (Bruce et al., 1999). It is worth mentioning however, that the initial soils were highly degraded after supporting cattle grazing for more that 12 years. Application of fertilizer was also very low to the systems. This suggests that there is space for increasing C accumulation rates through the practice of agroforestry.
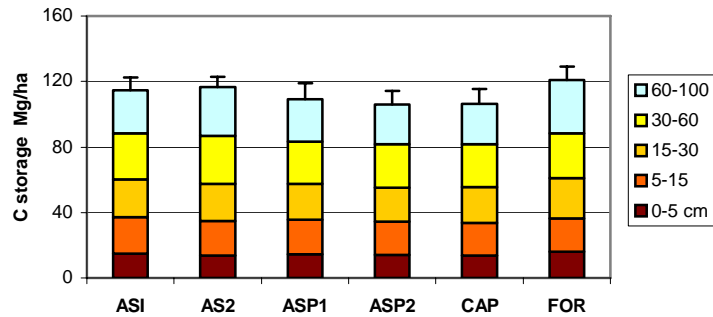
Figure 4. C storage in soil under various land uses in the Central Amazon

Conclusions

Charcoal is an ubiquitous constituent of the soils in the Central Amazon and appreciable amounts can be found even at 1 m depth. Coarse fragments are located preferentially at the surface layers showing high heterogeneity in its spatial distribution. Fine particles distribute rather homogeneously through the soil profile. Charcoal derived-C can account for as much as 15% of total soil C. Separation of coarse and medium size charcoal fragments is very important to allow appropriate comparison between SOC in different land use systems in areas where fire is a factor in the natural or human influenced management of the forest. Although charcoal separation and the assessment of black carbon is a time consuming process, given that charcoal is a remarkably stable pool, once a baseline has been established for a certain site, the same information could be used in future studies.

Though various studies have shown that soils under pastures enable high rates of C sequestration (Fisher et al., 1994) in our sites, the lack of fertilizer inputs and the high initial degradation of the land prevented a significant accrual of SOC as compared to soils under secondary vegetation.

Even under unfavorable initial conditions, agroforestry systems allow net C accumulation in soils, permitting the soils to move in a 10 years time period, from 87% to 95% of the total C stocks in the primary forest.

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Biodiversity and ecosystem services in agricultural landscapes – are we asking the right questions?

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Abstract

The assumed relationship between biodiversity or local richness and the persistence of 'ecosystem services' (such as sustained productivity and regulation of water flow and storage) in agricultural landscapes has generated considerable interest and a range of experimental approaches, but the abstraction level aimed for may be too high to yield meaningful results. Many of the experiments on which evidence in favour or otherwise are based are artificial and do not support the bold generalizations to other spatial and temporal scales that are often made. Future investigations should utilise co-evolved communities, be structured to investigate the distinct roles of clearly defined functional groups, separate the effects of between- and within-group diversity and be conducted over a range of stress and disturbance situations. An integral part of agricultural intensification at the plot level is the deliberate reduction of diversity. This does not necessarily result in impairment of ecosystem services of direct relevance to the land user unless the hypothesised diversity-function threshold is breached by elimination of a key functional group or species. Key functions may also be substituted with petro-chemical energy in order to achieve perceived efficiencies in the production of specific goods. This can result in the maintenance of ecosystem services of importance to agricultural production at levels of biodiversity below the assumed 'functional threshold'. However it can also result in impairment of other services and under some conditions the de-linking of the diversity-function relationship. Avoidance of these effects or attempts to restore non-essential ecosystem services are only likely to be made by land-users at the plot scale if direct economic benefit can be thereby achieved. At the plot and farm scales biodiversity is unlikely to be maintained for purposes other than those of direct use or '*utilitarian*' benefits and often at levels lower than those necessary for maintenance of many ecosystem services. The exceptions may be traditional systems where *intrinsic* or 'non-use' values continue to provide reasons for diversity maintenance. High levels of biodiversity in managed landscapes are more likely to be maintained for reasons of intrinsic ('non-use'), *serependic* or 'option' values or utilitarian (direct use') than for *functional* or 'indirect use' values. The major opportunity for both maintaining ecosystem services and biodiversity outside conservation areas lies in promoting diversity of land use in ways that meet these requirements at the landscape scale. This requires however an economic and policy climate that favours diversification in land-use products and diversity among land users.

Introduction

The role of biological diversity in the provision of ecosystem goods and services and the way this role can be valued and managed during agricultural intensification is much debated but still poorly understood. A key problem in all debates on biological diversity is that the abstraction 'diversity' has often not been distinguished from the specific attributes of the community of organisms that is under study in any particular location or system For instance if the interest lies in the functional roles of the community these may depend on the 'structure' of the vegetation and the relationships between different 'functional groups', rather than on diversity as such. Experiments based on random species assemblages may be appropriate tests for hypotheses about 'diversity' per se, but tell us very little about the largely self-selected assemblages that make up natural ecosystems. In the case of agro-ecosystems, whilst the dominant crops or livestock are artificial, by far the majority of the species are self-selected. So, are we asking the right question? Does the loss of diversity at plot-to-global scales imply a threat to critical ecosystem functions? Can we identify thresholds in such a process?

Global diversity derives from the lack of overlap in species, genetic or agro-ecosystem composition between geographic or temporal domains as embodied in the niche concept. While 'agricultural development' affects local (ie. plot level) diversity, it probably has even stronger effects by homogenizing at higher scales, facilitating the movement of 'invasive species' and the introduction and spread of 'superior' germplasm of desirable species. Scale is thus of overriding importance in our analysis and we may well find that answers may appear contradictory between different ways of defining temporal and spatial boundaries to the system under consideration. In this review we will first consider the concepts of 'biodiversity' and 'ecosystem functions', and then the evidence that links relevant aspects of the two, before we embark on an exploration of how this relationship depends on scale and can be 'managed'.

The biological basis of ecosystem goods and services

Humans have evolved as part of the world's ecosystems, depending on them for food and other products and for a range of functions that support our existence. Natural ecosystems, as well as those modified by humans, provide many services and goods that are essential for humankind (Matson et al., 1997). Efforts and interventions to manipulate (agro)ecosystems to meet specific production functions, represent costs to the rest of the ecosystem in terms of energy, matter and biological diversity, and often negatively affects goods and services that so far were considered to be free and abundant. These are anthropocentrically regarded as services because they provide the biophysical necessities for human life or otherwise contribute to human welfare (UNEP, 1995; Costanza et al., 1997). Most if not all of these services are based on a 'lateral flow', or movement across the landscape of biomass (such as food, fibre and medicinal products derived from the sea, inland waters or lands outside of the domesticated 'agricultural' domain), living organisms and their genes, or earth (nutrients), water, fire or air elements. Examples of ecosystem services particularly important for agroecosystems and agricultural landscapes are: maintenance of the genetic diversity essential for successful crop and animal breeding; nutrient cycles; biological control of pests and diseases; erosion control and sediment retention; and water regulation. At a global scale other services become important such as the regulation of the gaseous composition of the atmosphere and thence of the climate. A list of such services is given in the first column of Table 1 of the Appendix, and their connection to lateral flows is discussed by Van Noordwijk et al (Table x, this volume).

These ecosystem goods and services are biologically generated. The community of living organisms within any given ecosystem carries out a very diverse range of biochemical and biophysical processes that can also affect neighbouring systems. These can be described at scales ranging from the subcellular through the whole organism and species populations to the aggregative effect of these at the level of the ecosystem (Mooney and Schultze 1993). All ecosystems have permeable boundaries with respect to material exchanges but the within–system flows usually dominate those between systems, such as between land-use or land-cover types within a landscape. For purpose of this paper we define *ecosystem functions* as *the minimum aggregated set of processes (including biochemical, biophysical and biological ones) that ensure the biological productivity, organisational integrity and perpetuation of the ecosystem*. There are no agreed criteria for defining a minimum set of such functions but for the purposes of this paper the second column of Table 1 lists ecosystem functions alongside the ecosystem services they provide. Further explanation of these relationships is given below but it is useful to note that these functions can be pictured as having a hierarchical relationship. The energy captured in primary production is utilised in the herbivore and decomposer food chains. Interactions between these three subsystems occur through nutrient exchanges and a variety of biotic regulatory mechanisms as well as by energy flow. In particular the balance between the constituent processes of primary production and those of decomposition determines the amount of energy and carbon maintained within the system and is the major natural regulator of the gaseous composition of the atmosphere at a global scale (see Swift 1999).

Biological diversity and its values

Most discussions and empirical studies on biodiversity have focused on issues of a relatively small range of organisms. In contrast, the Convention on Biological Diversity defines its area of concern as:

" …the variability among living organisms from all sources, including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species, and of ecosystems" (Heywood and Bates, 1995). Diversity within each one of these three fundamental and hierarchically related levels of biological organisation can be further elaborated as follows: genetic diversity is the variation within and between species populations; species diversity refers to species richness, that is, the number of species in a site, habitat, ecological zone or at global scale; ecosystem diversity means the diversity of assemblages (and their environments) over a defined landscape, ecological zone or at global scale.

Biodiversity in this paper refers to the totality of the species (including the genetic variation represented in the species populations) across the full range of terrestrial organisms i.e. invertebrate animals, protists, bacteria and fungi, above- and below-ground, as well as the vertebrates and plants which often constitute the main concerns of biodiversity conservation. With a definition as broad and inclusive as this, it is highly unlikely that any clear and precise statements about relationships between 'biodiversity' and functions can be formulated and tested that can be helpful in guiding human activity. Similar to the situation with 'watershed functions' we may find that discussions on components of the overall biodiversity concept in relation to land use are more productive and open to progress than those that stay at the aggregate level. In the section immediately following we shall refer to the diversity within ecosystems (often termed alpha diversity) and in later sections to that at the broader scale of the landscape (which embraces concepts of both beta and gamma diversity).

The analysis of biodiversity and its management is highly influenced by the perspective used. In particular different sectors of society attribute different values to biodiversity. Broadly speaking four different types of value can be usefully recognised, although different terminology is often used..First is the **intrinsic** or 'non-use' value of diversity to humans, which comprises its cultural, social, aesthetic, and ethical benefits. Some groups in society attribute high social and religious values to individual species or communities of organisms; others derive value from the simple fact of high diversity per se in such systems as tropical rainforests or coral reefs. Second is the **utilitarian** or direct use value of components of biodiversity, i.e. the subsistence, financial and monetary benefits of species or their genes derived by one or other sectors in society. The direct use value may be private and accrue to the land managers (farmers, local community, government). This is most obvious with respect to high value agricultural crops but also applies to the other types of good listed in Table 1. For instance, the pharmaceutical industry values the tropical forest tree *Prunus africana* very highly because its bark contains chemicals used for manufacturing a drug. Another example is that in Africa, many farmers living near natural (and protected) forests withdraw substantial monetary benefits from their hunting and from collecting plants and tree products in these forests (Pottinger and Burley, 1992).

Thirdly, biodiversity can be said to have **serependic** or 'option' value. This is the belief in future but yet unknown value of biodiversity to future generations, for example the presence of a microorganism with an as-yet undiscovered genetic potential for industrial products. These three types of value of biodiversity are ethnocentric and depend very much upon the cultural values and preferences of different sectors of society. This is why some authors, interested in such values, stress that 'the conservation of biological diversity depends as much on society's ethical views as on facts' (Barrett 1993).

Finally, biodiversity and the integrity of processes that maintain and generate diversity have **functional** significance. This may be the 'indirect use' value of Kerry Turner (1999). Part of this functional significance may be of direct utilitarian value for *Homo sapiens* in the production of goods and services that can be priced. Beyond this lie a range of ecosystem services that are of acknowledged benefit to humans but which generally lie outside the boundaries of recognised utilitarian benefit. The purpose of this paper is to analyse the functional values of biodiversity with particualr reference to the diversity in agricultural landscapes but it also has a more general significance for life over and beyond this single species. This non-human significance, however, can only be translated into a 'value' that can play a role in human decisions via human 'champions' and thus cannot in practice be separated from the intrinsic value.

What is the relationship between diversity and function?

Concepts

Biologists have for many decades speculated on the question of why there are so many species of living organism. As explored in the theory of island biogeography, the diversity within any ecosystem at any point in time is the result of a 'self selection' process, that involves co-evolution of the species comprising the biological community within a given ecosystem by interactions among them and with the abiotic environment through time. This is not an isolated process. New species may enter an ecosystem from neighbouring areas, some establishing themselves and others failing to do so. Partly as a result of successful newcomers or new adaptations emerging in existing ones (be they competitors, predators, pests or diseases), and partly as a result of fluctuations in abiotic environmental conditions, some of the existing species may become (locally) extinct over any period of time. The species richness of any given ecosystem or land unit is therefore a dynamic property. In agro-ecosystems farmers take a dominant role in this dynamic by the selection of which organisms are present, by modifying the abiotic environment and by interventions aimed at regulating the populations of specific organisms ('weeds', 'pests', 'diseases' and their vectors and alternate hosts). The dynamic nature of the (local, patch level) diversity of any system, whether natural or agricultural, is often underrated, as is the importance of the selection pressure and process. The diversity of any system is not adequately represented simply by the number of species (or genotypes) present, but by the relationships between them in space and time. Attempts to assemble combinations of the same number of species under slightly different conditions and in particular without the history of interaction often fail (Ewel et al 1991). But what makes any existing species combination into a 'system' is still largely elusive. Some insights obtained in analysing food webs may help. For example Neutel (2001) showed that the majority of belowground food webs constructed from random combinations of organisms did not meet dynamic stability criteria, even though all parameters such as abundance of groups and dynamic properties were chosen in a 'normal' range when considered one-by-one. Yet, systems with the actual parameter combinations that are attained in the field do [DID?] meet stability criteria, suggesting that partly uncovered rules about the proportionalities and co-variance within the normal range are crucial.

Debate on the relationship between biological diversity and ecosystem function has a long history which has taken on new vigour (and sometimes even rancour) since the advent of the Convention on Biological Diversity (see Woodwell and Smith 1969 for the older literature and Schulze and Mooney 1993, Mooney et al 1995, 1996, and many of the citations below for more recent discussion). Vitousek and Hooper (1993) contributed a major focus to this debate through hypothesising three different possible relationships between plant diversity and broad-based ecosystem functions such as the rate of primary production (Figure 1). Their analysis of current evidence led them to propose that the asymptotic relationship shown as Curve 2 in Figure 1 was the correct one. This suggests that whilst the essential functions of an ecosystem, such as primary production, require a minimal level of diversity to maximise efficiency this effect is saturated at a relatively low number. Swift and Anderson (1993) proposed that this relationship could also apply to the decomposer system. Examples of essential functions in this case are the basic suite of catabolic enzymes (e.g. for cellulolysis, lignin degradation etc), the facilitation role that invertebrates play by reducing particle size by their feeding activity, and biophysical processes of pore formation and particle aggregation. It is interesting to note however that the communiies of organisms contributing to the ecosystem function of decomposition are taxonomically much more diverse than those of primary production.

Experimental approaches

Over recent years a number of authors have reported on experiments investigating the links between diversity and specific functions (e.g. see Ewel et al 1991, Naeem et al 1994, Naeem and Li 1997; Tilman and Downing 1994; Tilman et al 1996,1997; Hooper and Vitousek 1997) that appear to broadly corroborate the predictions of the Vitousek-Hooper hypothesis for primary production. This has however generated an equal amount of discussion in refutation and the issue remains significantly a matter of interpretation and opinion (see Grime 1997; Hodgson et al 1998; Lawton et al 1998; Wardle 2000; Naeem

2000). There is no space here to review these studies in detail. Each one of the experiments quoted can be criticised in one way or another. The strictest interpretation of many of the experiments would be that the conclusions apply only to the specific combinations of organisms used in the tests, and in most cases these are assemblages constructed for experimental purposes rather than naturally co-evolved communities. At a fundamental level such experiments suffer from a basic methodological paradox – in order to describe and understand diversity and complexity we need to simplify it, and take away the self-selection that governs real-world diversity. Dealing with the totality is impossible. For instance there is no single (or combination of) methods that would allow for the total inventory of the species richness of even a small volume of soil. It is thus difficult to draw general conclusions about 'diversity' as such and in particular with respect to naturally co-evolved communities. The results of such 'un-natural' experiments may however be more applicable to agricultural systems that in one sense can be said to have been assembled in a similar way.

The minimum diversity required within a functional group
One potentially valuable interpretation of the Vitousek-Hooper relationship has been that the minimal level of diversity required to maximise the production function consists of representatives of an essential set of 'functional groups' of plants. A functional group may be defined ' *a set of species that have similar effects on a specific ecosystem-level biogeochemical process'*. As Vitousek and Hooper put it the 'essential' plant species are those that contribute in different ways to the key ecosystem functions – in the case of primary production by exploiting different components of the available resources by differences in canopy structure to maximise light capture or symbionts and root architecture to optimise capture of water and nutrients. Drawing together the threads of this discussion we [hypothesise that?] suggest that *'the minimum diversity essential to maintain any given ecosystem function can be represented by one or a few functionally distinct species i.e. one or a few representatives of a small range of functional groups'* is a useful null-hypothesis to guide investigations of the functional significance of biological diversity in agricultural systems. It may need further operationalization for specific ecosystem contexts, however. The total diversity required then depends on the number of functions that are recognized and to the degree of overlap in 'functional groups' between these different functions.

Which functional groups of organisms are essential?
The functional group concept is briefly discussed in the Appendix to this paper and Table 1 lists a minimal set that we propose are needed to provide the ecosystem goods and services we have been addressing.

The classification of plants into functional groups has drawn a great deal of recent attention because of the recognition of the pressure being exerted on terrestrial ecosystems by global climate change (Smith et al 2000) The primary producers (together with the vertebrate herbivores) are our major source of food and are also the source of fibre and other useful materials such as latex. Molecules with antibiotic, therapeutic, pesticidal or similar biological activities utilised by humans are however synthesised by many groups of organisms (e.g. bacteria and fungi) and are often very specific in origin. Diversity is therefore an essential pre-requisite for maintenance of supply, particularly of new products, although the capacity to biologically generate or synthesise new compounds under laboratory conditions has been greatly increased by the advent of genetic engineering.

Decomposition and mineralisation of organic matter of plant and animal origin and synthesis and decomposition of soil organic matter are carried out by a very diverse community of invertebrates, protists, bacteria and fungi. Other elemental transformations often are carried out by a diverse set of functional groups with very specific biochemical capacities, for example certain of the bacteria of the nitrogen cycle. Diversity within these groups varies from very low to high, but it can be experimentally demonstrated that a single species per function may be sufficient under a given set of environmental conditions.

The dominant biological properties regulating water flow and storage in the soil are the plant cover, the soil organic matter content and soil biological activity. Macrofauna such as earthworms, termites and

other invertebrates influence the pore structure. Bacteria and fungi modify the extent of aggregation of soil particles. All these organisms and an additional range of decomposer organisms influence synthesis and decomposition of soil organic matter. Control of erosion and trapping of sediment is regulated by the architecture of the plants at and below the soil surface, the amount (and hence the rate of decomposition and movement) of surface litter, and the physical quality and organic matter content of the soil.

Under natural conditions the interactions between the populations of organisms at the various trophic levels i.e. plants, herbivores, symbionts, parasites, decomposers, predators and secondary predators result in a dynamic balance of population sizes. The total diversity is huge but any single population is only influenced by a relatively small number of interactions. Biological regulation of a specific pest, pathogen or disease vector of interest to humans is therefore dependent on a significant level of diversity among its parasites or predators. These in their turn may depend on other elements of diversity for their survival e.g. the presence of microhabitats, alternative hosts, nesting or egg laying sites, or refuges often provided by the vegetation.

Chemical transformation of toxic organic elements, chelation or absorption of basic elements and removal of toxic levels of nutrients or other chemicals from ground, running or soil water may be carried out by a diverse range of bacteria, fungi or protists often in association with invertebrates. In well-established waste disposal systems these organisms form 'guilds' which function in a very integrated way. As with decomposers distinct guilds may operate across different ranges of environmental gradients of temperature, pH, moisture, etc.

The earth's climate is regulated by the content of 'greenhouse' gases in the atmosphere –(CO_2, CH_4, $N0_x$, etc). Carbon dioxide is emitted or taken up under one circumstance or other by the majority of living organisms and is thus a phenomenon of such generality as to defy attempts to relate its dynamics to changes in diversity other than the totally catastrophic. Methane and the nitrous oxides are however the product and/or substrate for a relatively small number of bacterial species in the soil associated with soil, decomposing organic matter or the gut flora of animals. Diversity change may thus be more significant in these cases.

It is worth noting that even when the discussion of function-diversity relationships is reduced to considering only functional groups, the minimum extent of necessary diversity that is implicated is still very high.

What is the significance of diversity within functional groups?
If the above hypothesis is correct and ecosystem functions can be maintained by the minimal number of representatives of the essential functional groups then the questions remains as to what is the significance of the often high diversity within functional groups – which takes us back to the basic biodiversity question 'why are there so many species'? Answers to this question depend strongly on the scale of consideration. Different species often occupy similar ecological roles in geographically separated areas, and one of the major threats to local species is the lateral flow of organisms once such geographical barriers disappear. Replacement of local species by intrusive exotics does not necessarily change ecosystem processes, or local richness, although there are dramatic exceptions for specifically successful (from the perspective of the invader, at least) invasions. Such invasions are likely, however, to reduce global diversity and in fact have been identified as one of the major drivers of 'global change'

Vandermeer et al (1998) summarized the main issues in the discussion on the role of diversity in agro-ecosystems in the following three hypotheses of links between diversity and function:
1. Biodiversity enhances ecosystem function because different species or genotypes perform slightly different functions (have different niches);
2. Biodiversity is neutral or negative in that there are many more species than there are functions and thus redundancy is built into the system;
3. Biodiversity enhances ecosystem function because those components that appear redundant at one point in time become important when some environmental change occurs.

It is valuable to note that these are not necessarily mutually exclusive hypotheses, as they may refer to different space and/or time aspects of the system and the function of specific concern. We need to clearly separate the question of how the current diversity came into being (the 'self organization' of the system, based on the success in the evolutionary history of all component species) from the human or teleological perspective of the relevance of this diversity. Just as we have to distinguish between 'diversity per se' and 'diversity of actual systems', we have also to recognize that not all components of a system have the same probability of being lost as a result of simplification of agro-ecosystems and some functions may therefore be more resilient than others. Differences in life histories of the key groups of organisms confer different temporal and spatial contexts to their role in the ecosystem and their responsiveness to its self-organising properties.

The third of Vandermeer et al's (1998) hypotheses is extremely pertinent to the question of how much of this diversity is needed to maintain ecosystem goods and services in the face of agricultural intensification and other aspects of ongoing 'global change'. There is certainly substantial experimental evidence that the many key functions can be maintained by only small numbers of species within a particular functional group. For example monotypic cover by perennial plants can be as effective as a diverse community in controlling erosion. Although the decomposer community of a particular soil may be very diverse only a minority of the hundreds of species of fungi, bacteria or invertebrates participate in the decomposition process at a given time and place. The extent of redundancy implied by this can be demonstrated under laboratory conditions where decomposition can be fully mediated by single species cultures of enzymatically-diverse organisms such as white-rot basidiomycete fungi whilst in nature the same process may be carried out by several species of fungi, bacteria and animals (Swift 1976, Giller et al 1997).

The third hypothesis raises questions whether key functions can be maintained by one (and the same) species under all circumstances. This addresses the issue of the capacity of ecosystems to adapt to changing circumstances that result from elements of stress and disturbance. The capacity of a system to respond to and recover from disturbance is termed its resilience. This property has been attributed to the degree of connectivity within an ecosystem, a feature that depends at least in part on the composition and diversity (Holling 1973, 1986; Allen and Starr 1982). Diversity within functional groups may provide an important means for increasing the probability that ecosystem performance can be maintained or regained in the face of changing conditions. For the below-ground community for instance there is evidence that the same enzymatic function is carried out by different species of bacteria or fungi from the same soil under different, and even fluctuating, conditions of moisture stress or pH (see Griffin 1972 for discussion of this). In the case of plants different species may play a similar functional role in different seasons, under varying conditions of climatic or edaphic stress and in different stages of patch-level succession.

Resilience and diversity thresholds

Functional diversity thresholds are thus likely to be higher in the real world than in the relatively controlled situations under which most of the experiments on diversity-function relationships have been conducted. Recognition of the importance of diversity to the property of resilience suggests furthermore that the implication of equilibrium in the way that Figure 1 is drawn (see also figures 2 and 3) may be misleading. The shifts between different states of functional efficiency with changes in diversity are more likely to be rather abrupt. Perhaps a case could be made recognising resilience as an ecosystem service rather than a property. An alternative view, however, is to see resilience as a property which varies among functions rather than a unitary ecosystem property. The decomposition function for example, may be substantially more resilient than that of the regulation of specific pest populations.

Resilience is a concept that requires consideration of different spatial scales. The resilience of any local system after shocks that lead to local loss of diversity depends strongly on the ability of organisms to recolonize from the neighbourhood, and thus on the distance to the nearest suitable habitat and the dispersal of the organisms in question.

Managing biodiversity and ecosystem services in agricultural landscapes

What is the impact of agricultural intensification on biodiversity and ecosystem functions?
Our main concern in this paper is with biodiversity issues in agricultural landscapes i.e. landscapes containing agroecosystems. Agroecosystems can be defined as (natural) ecosystems that have been deliberately simplified by people for purpose of the production of specific goods of value to humans. The simplification down to one or a few productive plant or animal species is implemented for greater ease of management and specialisation of product to suit market demands, especially in highly mechanized forms of agriculture. In an ecological sense the system may be seen as one which is maintained by a high frequency of disturbance, in an early successional stage (Conway, 1993). In such systems a distinction has been made between 'planned' and 'associated' diversity (Swift et al 1996; GCTE 1997). The *planned diversity* is the suite of plants and livestock deliberately retained, imported and managed by the farmer. The composition and diversity of this component strongly influences the nature of the *associated biota* – plant, animal and microbial. The issue is more complex than the single issue of the extent of planned biodiversity that is maintained however. Agroecosystems are managed by substitution and supplementation of many of the natural ecosystem functions by human labour and/or by petro-chemical energy or its products. In addition to their direct effects on production these interventions provide the means to reduce the risk associated with reliance on ecosystem services, although it can be argued that this is serving to substitute one set of risks for another – that of dependence on the market. Furthermore whilst substitutions may buffer some of the functions they also run the risk of further damaging others. For instance the addition of pesticides may control diseases of immediate negative impact but also kill non-target organisms with other functions such as pollination or soil fertility enhancement.

During agricultural intensification the diversity of crops and livestock is reduced to one or a very few species of usually genetically homogenous species. The varieties are selected or bred for yield (e.g. high plant harvest index), taste and nutritional quality. Plant arrangement is commonly in rows, fallow periods are bare, sequences may be monospecific (varietal) or of two or rarely more species. This is in contrast to natural ecosystems where the genetic diversity of plants (both within and among functional groups) is high but varies in relation to environment. The effects of land use change and agricultural intensification on biodiversity and associated functions are still poorly understood but conversion to agriculture almost always results in fewer species of both planned and associated biota with lower genetic variation and representing less functional groups. Nonetheless the extent of diversity in even so-called monocultures may be underestimated by plot-level assessment of diversity at any point in time. A rapid interannual turnover of the germplasm is often employed to stay ahead of the evolutionary race with pests and diseases, adding a time dimension to diversity that may exceed evolution in natural systems, albeit with respect to a narrow genetic base. This varietal turnover depends however on 'externalized' functions of maintaining genetic diversity in gene banks, and on the mechanisms of rapid multiplication and transfer of such germplasm. This situation contrasts with that of extensive agricultural systems where diversity is deliberately maintained within the system with or without external exchange. Here a plot-level assessment may have more relevant boundaries of measurement, although lateral flows of organisms exist here as well. Production systems based on perennial crops and trees provide less opportunity for rapid turnover of varieties for obvious reasons, and there clearly is a much stronger need here for maintaining plot-level diversity as a risk management strategy (Van Noordwijk and Ong, 1999).

Primary production
Whilst many recent experiments have tended to confirm that community primary production may be maximised by a low-number diversity of functional types (see above) there is also abundant evidence that mono-typic stands can reach the same levels of production within relatively narrow environmental conditions. Biomass production is however not the only function or service performed by plants in ecosystems. The secondary functions related to ecosystem services may be more biodiversity-sensitive than that of food production. 'Intensive' production systems for specific high-value products (e.g. spices) can however be very diverse. Another exception may be in relation to pharmaceutical and agro-chemical

goods. Most products of these types are initially gathered from natural or secondary vegetation or derived from microbial cultures obtained from soil. Once the markets for such products are established, however, the required control over the concentrations of biologically active substances, and the opportunities for monopolization tend to favour more technically advanced modes of production. Maintaining global diversity is thus essential for both present and future needs although the synthetic capacity brought by the molecular biological revolution is fast rendering this less so. Herbivore diversity is highest in heterogeneous systems with high plant and resource diversity but monotypic vertebrate herds can reach equivalent levels of production in simplified grazing systems. Pest epidemics tend to occur in circumstances of low genetic diversity of the host plants or livestock.

Nutrient cycling
Nutrient cycles become more open in agricultural systems with losses of nutrient through offtake in harvest, run-off from compact surfaces, increased volatilisation through a changed surface environment and increased leaching associated with decreased soil organic matter content. These losses can be substituted by inorganic inputs but the efficiency of return to the plant is often low and fertilisation is usually required at levels far in excess of direct crop demand, which further exacerbates the losses and can leads to pollution of groundwater etc. There is substantial evidence demonstrating gains in crop productivity from nutrient additions through mixtures of organic and inorganic sources of nutrients compared with either alone (e.g. Swift et al 1994). Maintenance of organic inputs to the soil is thus an important management strategy for efficient use of external inputs. Advantages in utilising a variety of such inputs have also been demonstrated because of the strong influence of input chemistry (''resource quality') on patterns of mineralisation. The diversity of organisms involved in nutrient cycling may be substantially reduced under agricultural intensification but there is little evidence of significant effects on decomposition and mineralisation processes which has been attributed to a high level of functional redundancy among decomposer fungi, bacteria and microregulators such as nematodes or collembola (e.g. see Beare et al 1997, Giller et al 1997). The significance of this loss of diversity should not however be assumed to be inconsequential. In particular it is unclear how the resilience of the system under conditions of change is influenced by such loss. Organisms with very specific functions, such as those exhibited by some bacteria of the nitrogen cycle, often show specialisation to particular soil conditions such as pH and specific genotypes may be lost as a result of soil degradation. Specific strains of dinitrogen-fixing bacteria may also be lost a result of agricultural intensification resulting in the need for subsequent inoculation (Kahindi et al 1997).

Organic matter dynamics
Soil organic matter (SOM) is a keystone component of the ecosystem in the sense that its impact on overall system performance exceeds its relative share in the energy flow through the system. Soil organic matter (SOM) stores and buffers nutrient concentrations, influences water storage in the soil and is a major factor in determining soil structure and thence erosivity. Above all it is a store of energy in the soil that drives many of the soil-based processes. SOM synthesis and decomposition is brought about by much the same community of organisms as those involved in decomposition of plant litter. A well-charted phenomenon is the decline in SOM as a result of conversion of natural ecosystems to agriculture. Farmers utilize the nutrients mineralised as part of this decline of the SOM capital to support high initial levels of crop production after clearance. Soil tillage is also an effective additional way of stimulating the breakdown of SOM and plays a key role in promoting crop yields after land conversion to agriculture, until a new and lower equilibrium between breakdown and formation of SOM is reached. The level of the new SOM equilibrium, with its consequent impact on nutrient cycling, soil water regimes and erosivity, is related to the quantity of plant litter input, which is almost invariably lower than that of natural systems. Crops in intensive systems are usually selected for high harvest indices, and there may be uses for crop residues other than soil fertility maintenance (e.g. fodder or fuel). The SOM content is thus related to the quantity, diversity and mode of management of organic input to soil. A key feature of agroecosystem management is thus the trade-off between the gains in production from 'mining' the SOM versus the

potential negative impact on its other ecosystem services and in particular on system resilience. This 'trade-off' between the different values of SOM has been rarely recognised but become a matter of greater interest as society has begun to realize the potential value of sequestering carbon in soil as a means to slow down the rate of global climate change. A research question of continuing interest is whether the functional properties of SOM are in any way influenced by the diversity of organic materials from which it is synthesised.

Watershed functions

The most important factors regulating water infiltration and retention are the extent of ground cover by plants and/or plant litter. The reduction in these, including interposing of periods when ground is bare, leads to greater run-off and diminished infiltration as well as increasing the risk of erosion. Substitution by mechanical tillage can ameliorate as well as aggravate these effects. Monospecific cover can be just as effective as a divers one with respect to limiting run-off and erosion, trapping sediment and promoting infiltration, but to be effective it has to be present year round. Diversity of organic inputs is likely to have a positive effect by widening the probability of differences in timing of litterfall and rates of disappearance from the soil surface. As soil protection on slopes depends more on partially decomposed litter with good ground contact than on fresh leaves that can be easily washed away, the role of plant diversity on slopes is likely to be greater than on flat lands. The macrofauna moving between litter layer and soil strongly influence partitioning of water between surface runoff and infiltration as well as modifying water movement within soil. Interesting examples of the influence of these 'ecosystem engineers' show how circumstance specific diversity effects may be. Soil engineers making macropores in the soil are not welcome in all circumstances. In bunded rice fields, farmers make an effort to destroy soil structure by puddling to reduce the porosity of the soil and building dykes to contain the water. These earthworks may be destroyed by the actions of earthworms and surveys by Joshi et al. (1999) in the Ifugao Rice Terraces (IRT), in the Philippines showed that 125 out of 150 farmers interviewed ranked earthworms as the most destructive pest of terraced rice fields.   In a second example the conversion of Amazonian rainforest to pastures has been shown to lead to extinction of the natural earthworm community, which have been replaced in some circumstances by a single exotic species, *Pontoscolex corethrurus*. This has a negative effect on pasture productivity because the introduced worms compact the soil, whereas the native species improve soil structure (Chauvel et al 1999). Inoculation with species from the forest might reverse this effect, but remains to be tested.

Risks of pests and diseases

As already indicated the decreased genetic diversity of plant cover increases the risk of pest attack. Simplification of the ecosystem and in particular the use of broad-spectrum pesticides also decreases the diversity of natural enemies and increase risks of pest attack (Lawton and Brown 1993). Pesticides also have negative effects on non-target beneficial organisms including pollinators and beneficial soil biota.

Greenhouse gas emissions

Land-use change alters the balance of gas emissions and thence influences global climates. There are very large increases in the CO_2 output during clearing from natural vegetation and break down of soil organic matter reserves that are rarely if ever balanced by regrowth. The output of methane may be significantly increased in systems such as paddy rice and intensive cattle production and of nitrous oxides by N-fertilisation. These changes are linked to alterations in soil structure that dominate changes in the activity of a variety of soil organisms (e.g. methanogenic and methanotrophic bacteria) but we are not aware of any documented case where such effects are linked to the absence of functional groups or to biodiversity change per se.

A hierarchy of functions

There are a few general conclusions that may be drawn from this brief review of the impacts of agricultural intensification on the relationship between biodiversity and ecosystem services. *First* that

whilst there are a number of clear examples where changes in diversity have threatened the provision of ecosystem services, especially relating to the regulation of pests and diseases, there are also others where the changes in biodiversity seem to be functionally neutral, at least within relatively stable environmental conditions. *Second* there may be some functional groups, particularly micro-organisms such as the decomposers, where the degree of functional redundancy is such that the resilience of the function is very high. These two observations may be generalised by stating that there are no rules to be derived for agricultural systems concerning the importance of biodiversity with respect to the maintenance of ecosystem services that apply across all functional groups and environmental circumstances. Both the concept of 'diversity' and that of 'ecosystem function' are too broad to make generalizations at this level testable. There is a need and potential however to investigate the issues of thresholds of diversity-function relationship within specific functional groups and under circumstances of change in stress and/or disturbance.

Finally we should re-emphasise the importance of the hierarchical control exerted by the plants over the other functional groups (Figure 4, Appendix). This is a particularly important feature when determining management options, not only at the field and farm scale but also at that of the landscape. The plant, decomposer and herbivore subsystems of the biological community interact in a variety of ways but the productivity, mass, chemical diversity (resource quality) and physical complexity of the plant component exerts the strongest influence and is the single most important determinant of both the diversity and the functional efficiency of the other two subsystems. Wardle et (1999a and b) and Yeates et al 1999 showed for example that arthropod and microbial communities were not adversely affected by agricultural intensification provided the type of management (eg. mulching) provided for increases in the quantity and quality of the organic inputs. The maintenance of total system diversity and of the major part of the ecosystem services is thus predominantly determined by the nature of the plant community. This is also of course the main point at which humans intervene in the agroecosystem – to decide the species richness, the genetic variability and the organisation in space and time of the planned biota in the vegetation subsystem.

Implications for the design and management of agricultural landscapes
A substantial research investment has been made into agricultural systems that fall short of the full extent of genetic homogenisation and petro-chemical substitution. Examples are agroforestry and other inter-crops, rotations, mulch-based, minimum tillage and integrated livestock-arable systems. All these systems are characterised by maintenance of diversity of plant functional groups above the level of monocropping. The scientific justification for such approaches has generally been made on grounds of greater functional sustainability and the wider spread of risk associated with more diverse products as well as on the recognition that it is line with the management choices of the majority of the rural poor in the tropics. For farmers labour saving and low investment and risk may be the preferred attributes of these systems.

The simplicity of monocultures at field level is only possible as long as farms are part of a germplasm delivery system with rapid access to externalised gene banks and have access to risk buffering mechanisms such as insurance schemes or agricultural subsidies. Large parts of tropical agriculture still operate in a range where such 'externalized' risk management options do not exist and where thus a choice for monocultures carries unaffordable risks. At the farm level ecosystem resilience can be extended beyond resources maintained on farm or in the accessible neighbourhood by being part of a larger agricultural production and germplasm delivery system

Ewel (1986) and Moreno and Hart (1979) are among those who have advocated using plant functional groups as a basis for the (plot level) design of multi-plant agroecosystems. These designs also rely, explicitly or implicitly, on the impact that the effect of increasing the diversity of the vegetation system will have in enhancing the associated biodiversity both above- and below-ground and thence the probability of maintaining ecosystem services over a wider range of stress and disturbance. The evidence comparing such systems is almost entirely however based on assessments of yield, Vandermeer et al (1998) reviewed the literature on inter-cropping of all types and concluded that yield gains in comparison with mono-crops depends on the specific complementarities in resource use and seasonal development of

the components. As risks for the farmer depend on farm level diversity of potentially productive resources rather than on plot-level diversity, the focus of much agroecological research may have been too narrow.

Another key aspect that needs to be changed is the continuing separation of different aspects of management interventions on the base of disciplinary experience, such as soil or nutrient management from pest management. Interventions to ameliorate the impacts on any one of the different ecosystem services (as well as on productivity) are likely to influence others. Practices targeted at productivity but well documented in terms of their supportive, ameliorative or regenerative effect on other ecosystem services should be a top priority.

Does the relationship between diversity and ecosystem services change across scales?
Almost all the evidence that exists for the relationship between diversity and function is for the plot (and often the micro-plot or laboratory chamber) scale. But in order to provide policy makers with appropriate advice on the functional value of diversity it is necessary to consider the ways in which the three factors we have been considering – biodiversity, agricultural productivity and profitability, and ecosystem services – intersect at the landscape scale. Whilst the inter-relationships that we have described at the plot (patch) scale may help in understanding what happens at the landscape scale there is also the possibility that the rules change as one shifts across the scales. The productivity of any land-use system can be expressed on an area basis and the aggregate productivity across a landscape on the basis of the fractions occupied by different land uses. Biodiversity however has more complex scaling relationships and cannot simply be aggregated in this way. Nor can many of the functions that have been discussed here.

Much of the diversity in a landscape may exist at scales beyond the farm (between farm variability being larger than within-farm diversity), and the dynamics of diversity thus depend on the degree to which different farms remain (or become more) different. As agricultural research and extension have been based on the economies of scale that are perceived as attainable by homogenisation of farms with similar demands for inputs and services and similar outputs for markets, the trend in agricultural intensification has often resulted in the reduction of inter-farm diversity. This process is generally supported by policy interventions which tend to promote homogeneity in farmer goals, practice and behaviour, at least of over the short term. The agents of change in biodiversity beyond farm level are essentially different from those on farm.

In Figure 2 we hypothesise that the relationship between species richness and specific ecosystem services at the landscape scale may follow a relationship analogous with that of the Vitousek-Hooper model – together of course with all the attendant qualifications. That is to say that ecosystem services at the landscape scale are optimised by a diversity of land-uses, but the number that are required for optimisation is relatively small. If the hypothesis is correct then it would suggest that the presence of a relatively small number of different land-use types should be sufficient to satisfy the functional needs of the majority of ecosystem services. This generality needs however to be detailed for any given landscape into specifics with respect to not only the types but also their sizes, shapes, patterns on the landscape and practices of management.

It can be further hypothesised that at the higher scales of landscape and region the frequency and intensity of disturbance and stress (both natural and anthropogenic) is greater than those at the plot or farm scale and increasingly beyond the control of the land users. Prevention of decreases in the stability of agroecosystems and management of restoration become more difficult and costly and eventually become impossible from both biological and economic perspectives because connectivity is too high and disturbances too large. . The ecosystem services that enhance the resilience and adaptation of systems, such as biodiversity, thus become more and more important a feature of sustainable management as the scale of operation widens.

Figure 3 hypothesises a number of relationships implied in the above discussion. We have argued that at the plot and farm scales individual land managers and farmers manage biodiversity largely through simplification (i.e., by decreasing connectivity and maintaining agroecosystems at a stage of early succession) and substitution. Decreases in connectivity may, under specific conditions reach a threshold level of irreversibility, in which case the agroecosystem loses its resilience. However, the individual land

user can in most cases manage and control agroecosystem disturbances and stresses, such as pest outbreaks or sudden changes in relative prices, by making adjustments in the management of resources (land, water, germplasm, knowledge, labour, capital) at the farm scale. This is pictured as the shift from Curve 1 to Curve 2 in Figure 3, which hypothesises some of the scalar implications of the diversity-function relationship. We know, as shown for small-scale farms in Kenya by Osgood (1998), that many farmers do value genetic and species diversity on their farms, as they are aware that it minimises economic risk by enhancing on-farm diversification of plant and animal production. The history of agriculture provides many examples of how even extreme reductions in biodiversity can be managed, through periods of disturbance, by individual land users by substitution (e.g. chemicals, labour). Therefore, even though biodiversity has important ecological functions at the farm scale, it is nevertheless possible to decrease biodiversity levels very substantially at that scale while maintaining the productivity and resilience of agroecosystems. We postulate however that at higher scales the control and management of disturbances and stresses becomes more and more problematic and costly and the resilience function of biodiversity thus becomes an increasingly important issue in management.

Keep it simple: maintain ground cover
We have already emphasised the over-arching influence of the plant cover and diversity on the associated functional diversity and thence on the properties of resilience. The simplest rule for managing landscapes is thus to say that if the vegetation is diverse then the associated diversity and functions will be taken care of. The immediate implication of this is that monotypic landscapes – vast areas of the same crop or livestock system – are likely to be the most vulnerable to the same dangers to ecosystem services pictured earlier for the farm or plot scale. Examples of these effects are the pollution of ground water by nitrates and pesticides in large-scale chemical-based agriculture and the difficulty of controlling epidemics in genetically homogeneous stands of vast area. These however seem simply to be the same issues as those at the plot scale only writ larger. The mechanisms for correction are also the same – diversifying the type of land-use system in space and time.

Landscape mosaics
The majority of agricultural landscapes in the tropics, in contrast with most of the northern temperate zones, are indeed mosaics of different land uses. The most sensitive of the ecosystem services at the plot scale is probably the biological pest control system. The management opportunities for this increase with widening scale as greater opportunity for diversity in both genetic signals and physical structure of the vegetation permit a wider diversity and larger reservoir of control organisms. Many of the endangered invertebrates and microorganisms of the soil community are mobile, or may be carried by vectors, and can thus recolonise degraded areas from within mosaics that provide suitable reservoirs. Others (e.g. earthworms) are less so however and re-inoculations may be necessary. In each of these cases the size, pattern of arrangement and rotation in time of land-uses on the landscape will have significant effect on the efficiency of ecosystem service provision. Management at the landscape scale offers greater opportunity than at the plot and farm for varying land-use over time. Izac and Swift (1994) argued that sustainable land management could most easily be achieved at this scale by means of balance between aggrading and degrading areas i.e. between patches of high exploitation and those of fallow or rest. Soil organic matter change is a specific and far-reaching example. In areas of intensive production and harvest the soil carbon content may decrease but under fallow or tree-based production it can be re-built. The balance between these two options affect nutrient cycling, soil structure, water regimes and the emission of greenhouse gases. The policy requirements for such integrated management of landscape mosaics are however very different to the production-related approaches that currently prevail in favour of landscape homgenisation.

The third hypothesis of Vandermeer et al (1998) predicts that a higher diversity of species will be required to provide a buffer against stress and disturbance at the landscape scale than will be the case for any single patch within it (i.e. gamma diversity will be higher than the sum of alpha diversity). This is pictured in Figure 3 by the difference between curves 1 and 3. Humans can intervene relatively easily

(although not necessarily cost-effectively) at the plot scale to substitute for diversity loss – as represented by the difference between curves 1 and 2. At the landscape scale however intervention by humans, including these substitutive actions, will tend to widen the range of stress and increase the frequency of disturbance and further extend the diversity-function relationship (Curve 4 in Figure 3). Substitutive management for purposes of restoring ecosystem services (analogous to the Curve 1 to 2 relationship in Figure 3) is likely to be prohibitively expensive at this scale and may suffer from a 'free rider' problem where it is difficult to get all beneficiaries to share the costs. We contend therefore that the implication of this hypothesis is of very high risk associated with ignoring landscape scale management and focussing only on policies that promote plot scale interventions. Plot scale activities are more likely to exacerbate landscape scale problems than repair them. On the other hand landscape scale interventions offer great opportunity for improvements at the plot scale by increasing overall integration and resilience. There is thus more functional justification for arguing in favour of maintaining or enhancing biological diversity at the landscape scale than there is at the scale of the plot.

This model is of course simplistic and does not provide any guide to other features such as the size, shape and position (pattern) of patches on the landscape or on the temporal relationships between them. The hierarchical relationship between ecosystem services should assist in developing rules for these aspects. The regulation of erosion and water flows operates at a higher level in the hierarchy of controls than do aspects of nutrient cycling, soil structure and gas emissions or pest controls. Van Noordwijk et al (this volume) discuss these higher-level aspects of landscape management under the title of 'watershed services'. The lower level services such as nutrient cycles and biological control activities may then be built in through focus on aspects such as the degree of connection between the patches and the location, direction and intensity of the flows between them. It may be useful to classify land-use types into 'functional groups' in a manner analogous with that for species in order to develop more meaningful relationships between diversity and function at the landscape scale.

Policy implications
The changes associated with agricultural intensification, including the attendant processes of diversity reduction and substitution of function, are made in response to food need, market opportunity, and perceptions of increased management efficiency associated with mechanisation. These factors remain a dominant reality within market-orientated agriculture where a small number of specific products have high value and specialisation thus becomes a desirable target. Van Noordwijk and Ong (1999) discussed the paradox that urban consumers have access to an increasingly diverse array of food resources that are produced on specialized farms of greatly reduced internal diversity. Observed changes in diversity at a one scale may thus not represent changes at higher systems levels. The risks to agroecosystem services of simplifying ecosystems and substituting biodiversity by labour and chemicals (e.g., in pest control) are those of losing some keystone functions including the ability of an agroecosystem to adapt to change without further substitutive interventions. The evidence, as briefly described above, that ecosystem services might be significantly impaired in agroecosystems as intensification increases is substantial although the role of biodiversity is far from clearly understood. The farmer may not perceive these effects to be serious if the economic environment enables continuing profit based on subsidies related to the substitution process. This has been the basis of agricultural development in Europe and North America for many decades. It thus appears that to attain the essential goal of profitability, even without petro-chemical substitution, agroecosystem diversity is likely to be kept low and that associated with this low diversity there is a risk of crossing threshold levels for the maintenance of ecosystem services the restoration of which is likely to be extremely costly, let alone feasible. Decisions about the management of agroecosystems in market economies do not normally take into consideration the costs of interfering with ecosystem services, including those in which biodiversity plays a strong influence. But when agroecosystems are driven across thresholds from a desired to an undesirable state, the costs to society of being in this new undesirable state, or of restoration of a more desirable one if it is feasible, can be extremely high. Therein lies the risk of simplifying ecosystems. Holling (1986) provided a seminal analysis of the consequences of a number of such irreversibilities.

Policies for sustainable agriculture, i.e. to promote integrative practices that focus on the conservation of resources (including genetic diversity) as well as productivity, have proved elusive. If the policy needs are extended to include the management of biodiversity at the landscape scale in order to protect and enhance a wide range of ecosystem services, the problem becomes more acute. There are two particular reasons why the problem is exacerbated at higher scales. First, population pressure and globalisation of trade and the concomitant land use changes (expansion of cities into agricultural lands and of agriculture into marginal areas) result in increased frequency and intensity of disturbances and stresses by comparison with those at the farm scale. The capacity to correct these effects also diminishes because the sensitivity of the systems increases in concert with their connectivity as one moves up the hierarchy of scales (Holling, 1986).

Second, the higher the scale under consideration, the more difficult it is for the increased numbers of individual land users to develop an effective management strategy for agroecosystem disturbances, that takes ecological interactions and connectivity into consideration. Even at the scale of small watersheds, it is not often the case that land users have been successful in developing collective and effective means of control and management of disturbances. Furthermore, even if these land users have full knowledge of the relevant level of connectivity necessary to ensure resilience at the watershed scale, different sectors of society place differing levels of importance on ecosystem services and diversity. Farmers in tropical countries are unlikely to place as high a value on these functions of landscape diversity as does the community at large or the national society. They are furthermore highly unlikely to value the serependic (i.e. future) value of diversity, which is much more likely to be valued by national and global communities.

In economic terms, farmers value some of the on-farm benefits of diversity and very few of the off-farm benefits, for the usual reasons that costs and benefits outside of the managers' domain (i.e. externalities) are generally not taken into account by individual decision-makers. The argument is however not simply about off-farm effects of biodiversity being ignored. Farmer knowledge varies greatly. There may be for many a number of on-farm ecosystem services that farmers may be unaware of (e.g., the role of micro-organisms), and thus cannot value, as well as services they may be aware of but will not consider important (e.g., reduction of greenhouse gas emissions). The same services may be valued by other groups in society, with a different perspective and set of interests. What is a beneficial service for one group may also be a cost for another (e.g. the perception of earthworms as 'pests' for paddy rice farmers, the trade-off between carbon sequestration and SOM mining). For these reasons, management of ecosystem services, and of biodiversity at the landscape scale, as well as management of disturbances in agroecosystems in land use mosaics, is unlikely to be optimal, from either an ecological or an economic perspective, in the absence of specific policy or institutional interventions. Lack of knowledge of threshold levels in connectivity at different scales, different perspectives on the value of biodiversity, externalities and difficulties in large groups of land users coming together in developing effective means of controlling disturbances at the landscape scale thus result in biodiversity being managed by individual farmers in a sub-optimal manner.

We therefore conclude, on the basis of the relationships we have hypothesised earlier, that it will prove very costly to manage ecosystem services at the watershed, landscape and higher scales unless the functional value of biodiversity for productivity at the plot and farm scale and its interaction with 'externalities' beyond are perceived and valued. Furthermore, unless in particular the role of biodiversity in enhancing resilience is understood and factored into effective policy or institutional interventions, ecosystem diversity is unlikely to be maintained at the landscape scale without deliberate policy interventions at national and sub-national levels which take into account the real value of maintaining ecosystem services, given the externalities they generate and given their contribution to resilience. The biggest challenge is in the realization that most of diversity as well as much of its positive role in resilience probably exists beyond the farm scale, and that thus diversity of management decisions by farmers rather than any specific management system is key to its maintenance in the landscape. These policy implications and the need for diversity enhancing communal action remain largely unexplored territory.

There are two final comments that can be made to close this discussion. First that the absence of clear evidence should not be taken as evidence for the absence of effects and thus as a reason for doing nothing. Some economists have proposed that, in view of our relatively poor understanding of the exact roles of biodiversity in ecosystems on the one hand and of the potentially devastating effects of biodiversity loss on the other hand, a precautionary principle should be used in managing diversity. This principle acknowledges that while we may not be able to justify what some see as redundant species, there may be an extinction threshold that would result in an unacceptable level of ecosystem failure. Consequently, extreme care and precaution must be taken, and it is preferable to err on the conservative side (Perrings, 1991). The precautionary principle introduces an important concept, namely that of the risk of managing agroecosystems in such a way that threshold levels of biodiversity loss in relation to ecosystem services are ignored. The 'risk premium' that the precautionary principle suggests is hard to quantify as yet. Second that even if the evidence that high levels of biodiversity are not important for maintenance of ecosystem functions or services holds, that does not contradict the valuation of biodiversity for other reasons.

Concluding remarks

In the above discussion we have quoted or proposed a range of hypotheses concering the relationships between biological diversity and ecosystem functions, and their implications for the management of agriultural landscapes. The general relationships that have been proposed may have to be replaced by more specific hypotheses of the relation between components of overall biodiversity and specific environmental functions, bounded in space ant time. Sweeping generalizations from experiments that are necessarily restricted in space and time, and for example do not include major parts of the diversity-generating processes (including 'lateral flows' of dispersal and migration for re-establishment), are unlikely to be helpful in guiding the development of agro-ecosystems that have to provide for short, medium and long term service functions. Future investigations should utilise co-evolved communities, be structured to investigate the distinct roles of clearly defined functional groups, separate the effects of between- and within-group diversity and be conducted over a range of stress and disturbance. This might include: testing the basic functional-biodiversity rule by experimentally determining the minimal level of diversity between and within functional groups that is necessary to maintain productivity, integrity and perpetuation of ecosystems; characterising the functional groups of organisms necessary to maintain specific ecosystem services; determining the ecosystem function and service effects that ensue from elimination or substitution of key functional groups, including particular investigation of controls over below-ground diversity and function exerted by particular plant functional groups and other keystone organisms; and determining (and developing indicators for) the biodiversity thresholds for different ecosystem services. An interesting extension of the latter study might be to investigate whether similar thresholds exist for the intrinsic, utilitarian and serependic values of biodiversity.

Society as a whole has an interest in ecosystem services that are manifested substantially at scales above that of the field plot or farm. At the scale of the watershed or landscapes there is, in comparison with any single patch, a greater range of environmental stress and higher frequency of disturbance, including of extreme events. The maintenance of ecosystem services at these scales thus requires either a higher diversity of species within functional groups or a greater investment in substitutive management to maintain ecosystem services. These increments in diversity and/or investment are unlikely to be simply additive in view of the significant shifts in complexity that occur with shifts across scale. Optimal maintenance of ecosystem services at the landscape scale may be most readily achieved by a mosaic of a relatively few land-use types. This model is however likely to be overly simple because of: (a) differences in functional impact of different land-use types; and (b) the importance of organisation at the landscape scale in terms of the size, shape and location pattern of the constituent land-uses.

In developing appropriate land-use scenarios landscapes should be compared with respect to the aggregate values of their component land-uses for intrinsic, utilitarian and functional (ecosystem service) values of biodiversity. This would be assisted by establishing a typology of land-uses in terms of their efficiency in maintaining ecosystem service and in the trade-offs between this and profitability. The

results of the ASB project provide a model for this approach with respect to the interactions between carbon sequestration potential and profitability. The relative costs and benefits of segregating the intrinsic, utilitarian and functional uses of biodiversity between different land-use or landscape units compared with integrating them within such units is another parameter that should be of significant value for policy development.

This review confirms two unsurprising but crucial elements for policy development: first that whilst a number of important analogies can be drawn across scales with respect to the management of the relationships between biodiversity and ecosystem services, there are also emergent properties that necessitate different approaches; second that the value placed on the relationship between biodiversity and function (ecosystem services) by individual land-users is markedly different than those perceived by the community at different levels of society. We have indicated a number of biological and socio-economic issues that need to be clarified in order to provide more explicit advice to policy makers. No single optimal value can be placed on the biodiversity within a landscape. Land-use decisions are likely to be optimised if decision makers can be provided with scenarios showing how various land-use combinations result in different levels of diversity and the efficiency of different ecosystem services. In so-doing it will be important to include aspects of temporal change as well as pattern on the landscape as both these factors influence the resilience of the landscapes which should be regarded as a factor of over-riding importance. These scenarios can then be used to identify policy interventions and institutional arrangements necessary to achieve the desired objective, whether it is one dominated by agricultural productivity targets or the maintenance of ecosystem services or the conservation of biodiversity, or a combination of all three.
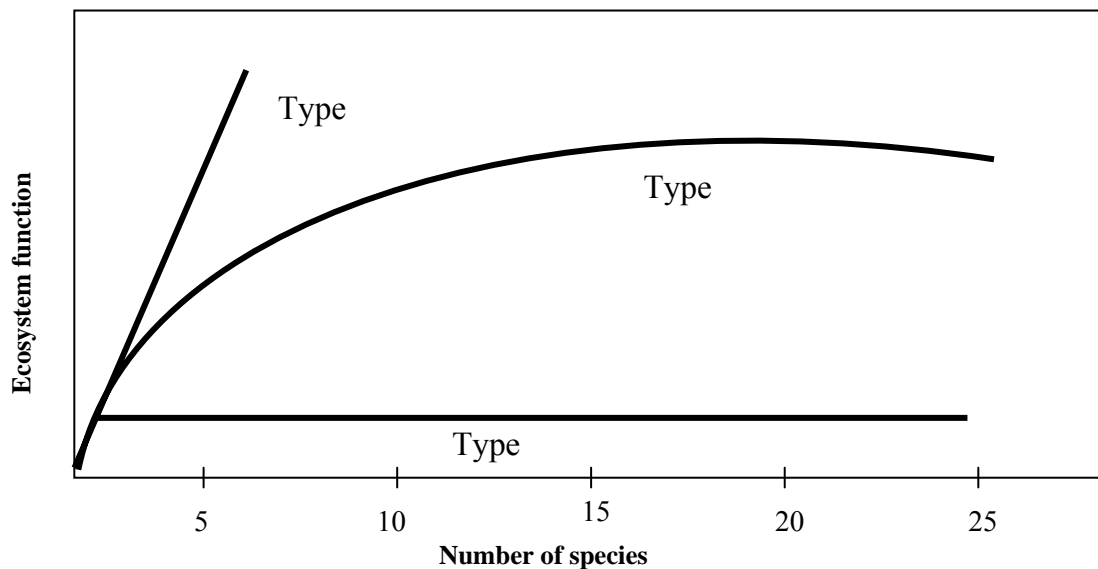

Figure 1: Possible relationships between biological diversity and ecosystem functions for the plant subsystem (from Vitousek and Hooper 1993). The authors hypothesised that curve 2 was the most probable of the three propositions.
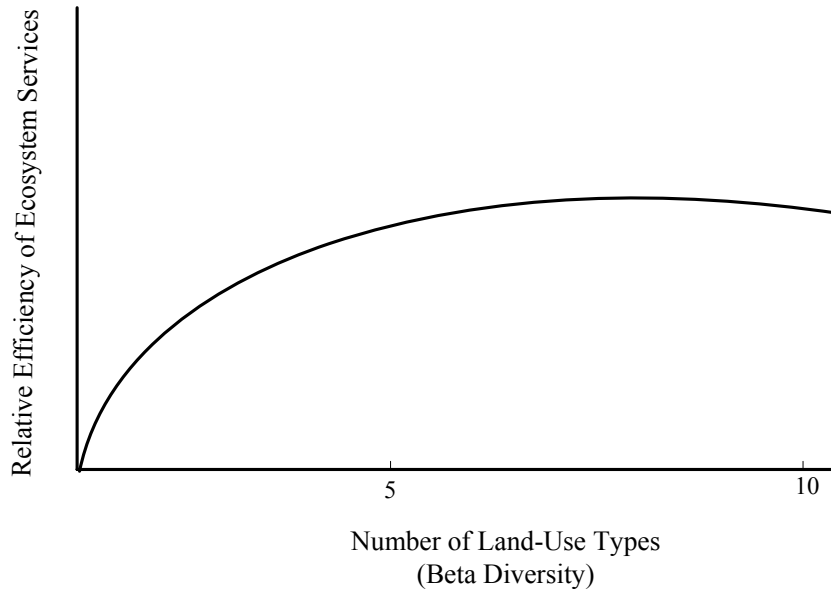
Figure 2: Hypothesised relationship between the diversity of ecosystem or land-use types and the efficiency of function of (the totality of) ecosystem services at the landscape scale.
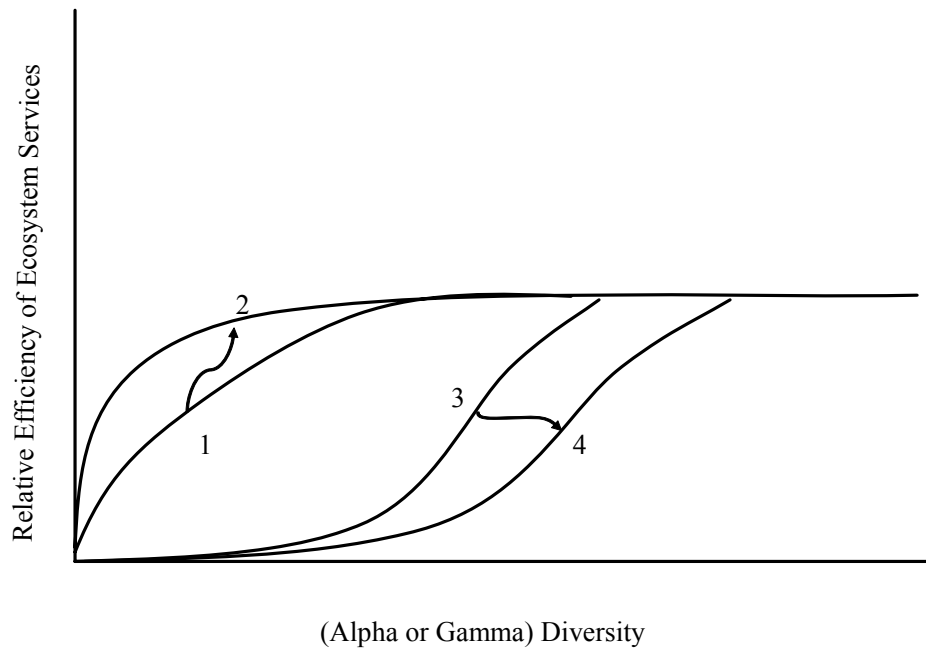

(Alpha or Gamma) Diversity

Figure 3: Hypothesised relationships between diversity (as measured by species richness) and the efficiency of function of ecosystem services at the patch-ecosystem (i.e. plot) scale (Curves 1 and 2) and the scale of the landscape (Curves 3 and 4). Curve 1 repeats hypothesis 2 of Figure 1: Curve 2 shows how in an intensively managed agricultural plot ecosystem services may be maintained by substitution of diversity by inputs derived from human and petro-chemical energy. Curve 3 shows, by comparison with curve 1, that the threshold of 'essential' diversity is greater as the land area increases. Curve 4 represents circumstances of high disturbance of the landscape by human intervention.
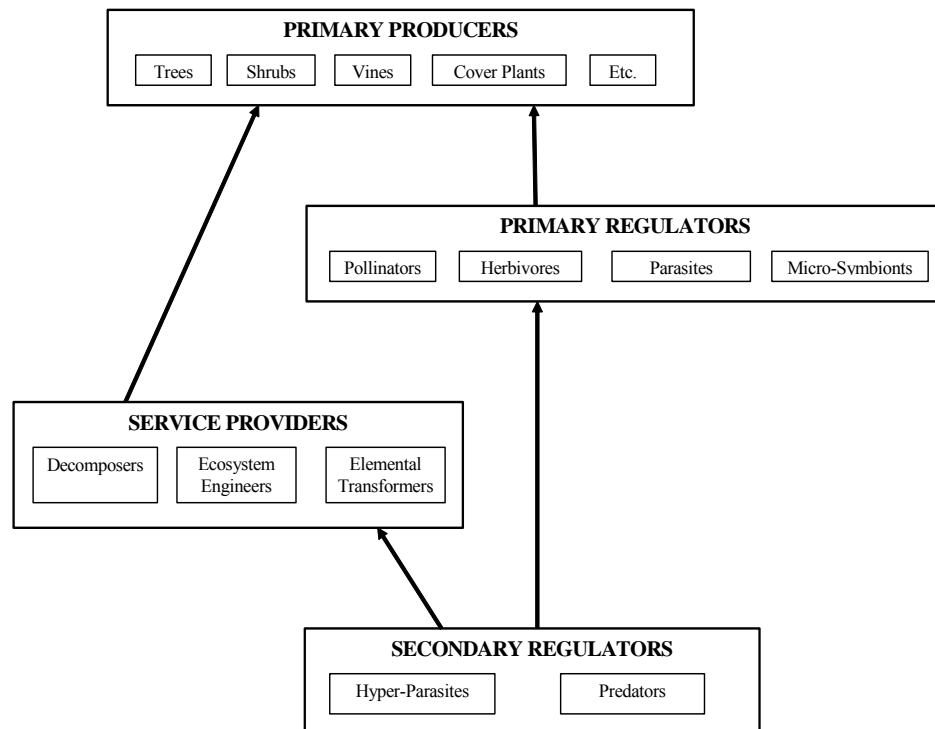
Figure 4: Hierarchical relationships between different categories of Functional Group – see Table 1 and Notes.

Appendix

Key functional groups: a preliminary classification

We have defined a Functional Group in text as ' a set of species that have similar effects on a specific ecosystem-level biogeochemical process'. There are many examples of classification of species in this way within specific taxonomic or trophic groups (e.g. for plants or pests). . There is no single classification to suit all purposes. In each case it is clear that the number of functional groups that is recognised, the criteria that are used to classify them and the degree of sub-division that is applied is a function of the question that is being addressed. We propose here a classification into the ten major groups that are briefly described below, together with such sub-division as may be necessary, for the purposes addressed in this paper, i.e. the relationships between biodiversity and function with particular respect to agriculture and ecosystem services. These Key Functional Groups are listed in Table 1 in relation to the ecosystem services they provide. The relationships between them are pictured in Figure 4. We suggest that this could provide a useful framework for investigating and testing key questions on this topic. A hierarchical structure is suggested (Figure 4). At the highest level are four major categories related to major trophic functions at the ecosystem scale i.e. Primary Production, Primary Regulation, Service Provision and Secondary Regulation. At the next level are the ten groups listed in Table 1 that perform distinct ecosystem functions; and at the third level are sub-divisions which it may be functionally and/or taxonomically useful to distinguish (e.g. vertebrate grazers versus invertebrate pests among the herbivores). Further levels of subdivision may also be useful or necessary in some cases.

Table 1: Relationship between key functional groups of organisms, the ecosystem level functions they perform and the ecosystem goods and services they provide

ECOSYSTEM GOODS AND SERVICES	ECOSYSTEM FUNCTIONS	KEY FUNCTIONAL GROUPS
Ecosystem goods including:		
Food	Primary and secondary (herbivore) production	Plants, Vertebrate herbivores
Fibre and Latex	Primary production and secondary metabolism	Plants
Pharmaceuticals and Agro-chemicals	Secondary metabolism	Plants, Bacteria and Fungi (Decomposers etc)
Ecosystem services including:		
Nutrient cycling	Decomposition Mineralisation and other elemental transformations	Decomposers Elemental transformers
Regulation of water flow and storage	Soil Organic Matter synthesis Soil structure regulation – aggregate and pore formation	Decomposers Ecosystem Engineers
Regulation of soil and sediment movement	Soil protection Soil Organic Matter synthesis Soil structure maintenance	Plants Decomposers Ecosystem engineers
Regulation of biological populations including diseases and pests	Plant secondary metabolism Pollination Herbivory Parasitism Micro-Symbiosis Predation	Plants Pollinators[1] Herbivores[1] Parasites[1] Micro-symbionts[1] Hyper-parasites[2] Predators[2]
De-toxification of chemical or biological hazards including water purification	Decomposition Elemental transformation	Decomposers Elemental transformers
Regulation of atmospheric composition and climate	Greenhouse gas emission	Decomposers Elemental Transformers Plants Herbivores

Notes to Table 1.

Primary Production
In some ecosystems photosynthetic micro-organisms may constitute as significant group eg. rice ecosystems). Here we deal only with plants.

Note 1.
Plants. There is a long history of classification of plants into functional groups. The groupings have been based on a variety of reproductive, architectural and physiological criteria. For the purposes of this paper the efficiency of resource capture is suggested as the main criterion. This will be determined by features of both architecture (eg. position and shape of the canopy and depth and pattern of the rooting system) and physiological efficiency. A very simple classification could for instance distinguish the roles trees, shrubs, vines and cover plants etc. and then subdivisions within each of these groups. Much more detailed consideration of these aspects is given by Smith et al (1997).

Primary Regulation (Note 1).
These are a set of functional groups which have a significant regulatory effect on primary production and therefore influence the goods and services provided by the plants.

Pollinators. See (ref) for discussion of functional groups of pollinators.[REFS BEING SOUGHT FOR THIS]

Herbivores: A great variety of organisms feed directly on primary producers. Vertebrate grazers and browsers are readily distinguished from invertebrate pests although their impacts on the plants may have similar functional significance at the ecosystem level. Each of these major groups are sub-divisible in terms of, for instance, feeding habits. The balance between different types of browser for instance can influence the structure of the canopy.

Parasites: Microbial infections of plants may limit primary production in analogous manner to herbivory. Parasitic associations can also influence the growth pattern of the plants and thence their architecture and physiological efficency.

Micro-symbionts: There is a wide range of microbial infections that are beneficial rather than destructive of which the most familiar are di-nitrogen fixing bacteria and mycorrhizal fungi.

Service Provision.
The functional groups within this category also strongly influence primary production but not in the directly destructive or stimulatory way of the primary regulators. They also provide a set of ecosystem services distinct to those deriving mainly from the primary producers.

Decomposers: This is group of great diversity which can be sub-divided taxonomically (bacteria, fungi, invertebrates etc) and in relation to size both of which correlate somewhat with functional roles in the breakdown (eg. detritivorous invertebrates) and mineralisation (fungi and bacteria) of organic materials of plant or animal origin (Swift et al 1979, Lavelle and Spain 2001).

Ecosystem Engineers: These are organisms that change the structure of soil by burrowing, transport of soil particles and formation of aggregate structures. The term is often confined to the macrofauna such as earthworms and termites but fungi and bacteria also play a key role in the binding of soil aggregates. Many of these organisms also contribute to the processes of decomposition.

Elemental Transformers: This may be the most diverse group of all and deserving of substantial subdivision. It includes a range of autotrophic bacteria that utilise sources of energy other than organic matter and therefore not classifiable as either decomposers but play key roles in nutrient cycles as transformers of C, N, S etc (eg ….). In addition there are heterotophs that thus have a decomposer function but also carry out elemental transformations beyond mineralisation (eg. free-living di-nitrogen fixers).

Secondary Regulators (Note 2)
Hyper-Parasites and Predators: This is diverse group of microbial parasites and vertebrate and invertebrate predators that feed on decomposers, herbivore, pollinators etc. They have particular significance in agriculture because of the service of biological control of pests and diseases that they play.

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