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Forest savanna ecotone dynamics in India as revealed by carbon isotope ratios of soil organic matter

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Abstract In India, the stability of the forest savanna boundary (ecotone) has been questioned. To investigate the possibility of vegetation change at this boundary, we used the natural difference in the stable carbon isotope ratio ($^{13}C/^{12}C$, expressed as $\delta^{13}C$) of C_3 (forest) and C_4 (savanna) plants, which is preserved in the isotopic composition of soil organic carbon. Past changes in the position of the ecotone can thus be documented by $^{13}C/^{12}C$ analysis of soil organic matter (SOM). Measurements were made on soil samples taken along a transect across the forest savanna boundary. In both ecosystems, $\delta^{13}C$ values of SOM in upper soil layers appeared to be in equilibrium with the current plant community: SOM was near −14‰ under savanna cover, and near −28‰ under forest. By contrast, $\delta^{13}C$ values of SOM from deep layers of soil profiles under forest cover near the ecotone, were less negative than would be expected for a C_3-dominated community. These results indicate that a change in ecosystem dominance occurred recently, and that forest has invaded an area occupied previously by a C_4 plant community (savanna and cultivated grassland).

Key words Soil organic matter · Forest-savanna ecotone dynamics · ^{13}C natural abundance · India

Introduction

Forest savanna boundaries varied widely during geological times, and shifts between these two ecosystems were rapid and controlled by climatic changes (Schwartz et al. 1986; Quade et al. 1989). Woody plant dominance in savannas and grasslands has increased recently in many parts of the world (Vuattoux 1976; Menaut 1977; Archer 1990; Dauget and Menaut 1992). The origin and recent dynamics of savannas and forest ecosystems are of prime importance in a country as populated as India, where deforestation is occurring at a rapid rate. Most savannas may have an anthropic origin (Pascal 1988) but palynological studies (Singh et al. 1990; Caratini et al. 1991) have shown an increase in the percentage of pollen of savanna species as early as 4000–3500 BP, remaining almost constant up to the present. These authors argue for a recent development of the savanna, linked to a decrease in rainfall. In contrast, Misra (1983) suggested that forests in India are favoured by present climatic conditions, and Pascal (1988) observed that plots protected from fires show increasing woody plant density.

Vegetation change has numerous consequences for the physical, chemical and biological properties of soil, especially soil organic matter (SOM). An important question is whether the re-establishment of the forest ecosystem is possible once the plot has shifted to savanna (after anthropic deforestation, and cultivation or grazing). These questions are difficult to answer using only the classical botanical and palynological approaches. The study of the natural ^{13}C content of SOM allows us to provide direct geochemical evidence for the occurrence of shifts in C_3/C_4 composition at a given site through time.

Study site and methods

The study was carried out in the Western Ghâts (13° 56′ 49″ N, 74° 44′ 20″ E). The climate is characterized by a mean annual temperature of 22.5° C and an average monsoonic rainfall of 5000 $mm.year^{-1}$, concentrated between June and September. In this area, the steep escarpment of the Western Ghâts is covered by evergreen forest, where the site of Chandemane (540 m) has been selected as a reference. On the backslope, numerous small hills are covered by pasture at the top, and by forest (intermediate between evergreen and moist deciduous) at the bottom. At the Kattinkar site (alt: 600 m) a toposequence (350 m in length) across these two

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Table 1 Vegetation, litter and soils characteristics of the study sites

	Chandemane forest	Kattinkar forest	Kattinkar savanna
Vegetation	Evergreen forest of *Dipterocarpus indicus-Diospyros candolleana-Diospyros oocarpa* type maximum height: 40–45 m	More or less degraded form of the same evergreen forest maximum height: 20 m	Continuous grass layer interspersed with trees. Three abundant C_4 grasses: *Arundinella holcoïdes* *Arundinella pumila* *Ischaemum indicum*
Litter ($t \cdot ha^{-1}$)	10.6 ± 3.1	9.3 ± 3.1	
Organic matter:			
C ($mg \cdot g^{-1}$ surface horizon)	54	46	26
N ($mg \cdot g^{-1}$ surface horizon)	4.0	3.1	1.7
C/N	14	15	15
Stock ($kg \cdot m^{-2} \cdot m^{-1}$)	9.8	6.0	4.4
Clay (%)			
Surface horizon	45	38	26
B horizon	43	52	33
Soil Classification:			
CPCS	Ferrallitic soil, weakly desaturated, rejuvenated	Ferrallitic soil, moderately desaturated, impoverished	Ferrallitic soil, strongly desaturated, impoverished
Soil taxonomy	Ustic Dystropept	Plinthustalf	Typic Haplustult

types of vegetation has been studied in order to document the ecotone dynamics.

The soil mantle is ferrallitic, rich in kaolinite and iron oxides. The principal features of vegetation, litter and soil in Chandemane forest, Kattinkar savanna and Kattinkar forest are summarized in Table 1. Vegetation at the Kattinkar forest was similar to that at Chandemane, with more than half of the species found in both locations. Soil profiles were studied and sampled in pits which were dug to a depth of 2 m. A more detailed analysis of these soils is presented in Peterschmitt (1991). The field study has not revealed any evidence of recent accumulation. The high amount of gravel, limiting the root penetration, is in good agreement with the assumption that older organic matter is located deeper in the profile. As observed in Table 1, upper horizons of savanna soils are impoverished due to loss of clays and SOM.

Isotopic ratios of SOM were measured on a system composed of an elemental analyser (CHN NA 1500, Carlo Erba) coupled to a Fisons SIRA 10 Isotope Ratio Mass Spectrometer (Girardin and Mariotti 1991).

Results are expressed in $\delta^{13}C$ versus PDB standard:

$$\delta^{13}C‰ = \left[\frac{{}^{13}R_{\text{sample}}}{{}^{13}R_{\text{standard}}} - 1\right] \cdot 1000 \quad \text{where } {}^{13}R = \frac{{}^{13}C}{{}^{12}C}$$

Repeated measurements yielded a precision (1σ, 8 aliquots) of 0.06‰ for a soil standard ground carefully and homogenized. Variability linked to sample heterogeneity is greater than analytic precision, so we sieved and homogenized all samples and performed isotope analysis on granulometric fractions < 100 μm.

^{14}C measurements of SOM of a forest profile in Kattinkar were performed by liquid scintillation counting (Balesdent and Guillet 1982), in order to test the assumption that older organic matter is located deeper in the profile.

The natural difference in the stable carbon isotope composition of C_3 and C_4 plants provides, via the study of SOM isotopic composition, an opportunity to assess vegetation change in areas where forests (C_3 plants) and tropical grasses of savanna (C_4 plants) coexist. Carbon isotope fractionation associated with photosynthesis is less for C_4 plants than for C_3 plants. This results in a characteristic isotopic composition in plant tissues: $\delta^{13}C$ values of C_3 plants are between -23 and -34‰ (average of -26‰) whereas C_4 plants range from -9 to -17‰ (average of -12‰). In the same location, the average difference between C_4 and C_3 plants is approximately 14 ‰ (Bender 1968; Smith and Epstein 1971; O'Leary 1988).

Numerous studies (Troughton et al. 1974; Goh et al. 1976, 1977; Flexor and Volkoff 1977; O'Brien and Stout 1978; Schleser and Bertram 1981; Stout et al. 1981; Dzurec et al. 1985; Nadelhoffer and Fry 1988; Martin et al. 1990; Mariotti 1991; Balesdent et al. 1993; Mc Pherson et al. 1993) demonstrate that the isotopic composition of SOM is similar to the vegetation growing on the soil, but generally with a slight increase of several ‰ with depth. The main control of $\delta^{13}C$ of SOM is plant litter inputs; however, other factors can affect this source isotope composition, such as isotope fractionation during decomposition and humification. Blair et al. (1985) observed in an in vitro culture of *Escherichia coli* that respired CO_2 is ^{13}C-depleted by 3.4‰ compared with the substrate (glucose). Loss of ^{13}C-depleted respiratory CO_2, by mass balance effect, can enrich the residual SOM in ^{13}C (Kaplan and Rittenberg 1964).

Differential preservation of ^{13}C-enriched SOM components could potentially account for the pattern of ^{13}C enrichment with depth. Isotopic differences between various biochemical fractions of up to 5‰ are reported (Deines 1980; Benner et al. 1987). Nadelhoffer and Fry (1988) noticed that labile fractions (holocellulose, water soluble fractions) are ^{13}C-enriched relative to plant tissues, while lignin, the fraction most likely to be preserved during SOM decay, is ^{13}C-depleted. These observations would support a ^{13}C depletion rather than the observed ^{13}C enrichment with depth.

Due to recent variation in the ^{13}C content of atmospheric CO_2 (Friedli et al. 1986; Marino and McElroy 1991), changes have occurred in the litter isotopic composition during the last century. These variations are < 1.2‰ and could partially explain the SOM ^{13}C enrichment with depth (assuming older organic matter is always located deeper in soil profiles).

Illuviation of ^{13}C-enriched dissolved organic matter (Nadelhoffer and Fry 1988) into lower soil horizons is also a possible key to understanding ^{13}C enrichment of SOM with depth. But these fractions are very labile, quickly metabolized and not preserved, and SOM ^{13}C enrichment has been observed (Nadelhoffer and Fry 1988) even in laboratory incubation, without any illuvial input.

Although SOM becomes ^{13}C-enriched with increasing depth (and age) in the soil profile, it should be noted that this enrichment is always < 4‰, not large enough to mask the 14‰ difference between C_3 and C_4 plant litter. Therefore, given the time limits imposed by the turnover rate of SOM, it is possible to determine with ^{13}C content of SOM profile if a change in the C_3/C_4 composition of a plant community has occurred (Krishnamurthy and De Niro 1982; Dzurec et al 1985; DeLaune 1986; Schwartz et al. 1986; Guillet et al. 1988; Mariotti and Balesdent 1990; Ambrose and Sikes 1991; Tieszen 1991; McPherson et al. 1993; Wang et al. 1993).

Table 2 Carbon isotopic composition of the vegetation in the studied zone

			δ^{13}C vs PDB
Kattinkar savanna			
	Grasses	*Arundinella holcoïdes*	−11.4
		Arundinella purpurea	−11.2
		Ischaemum indicum	−11.5
	Trees	Leaves (mixture)	−27.1
		Litter of savanna trees	−26.8
Border			
	Shrubs	Leaves of *Strobilanthes* sp.	−31.5
Kattinkar forest			
	Tree leaves	*Garcinia indica*	−31.7
		Psychotria truncata (<10 m)	−31.5
		Dinocarpus longan	−31.1
		Persea macrantha (>10 m)	−31.1
	Litter	Mixture of whole leaves	−29.6
		Mixture of fragments of leaves	−29.6
		Branches (<2 cm)	−30.9
		Branches (>2 cm)	−29.4
		Fragments of branches	−29.3
		Mixture of fruits	−29.3
		Unidentified organic matter:	
		– (>2 mm)	−29.3
		– (<2 mm)	−29.0
		Earthworms fecal pellets	−28.3
Chandemane forest			
		Mixture of tree leaves	−31.9

Results and discussion

Table 2 presents the δ^{13}C values of the most abundant plant species in the ecosystems studied.

In Kattinkar, all grasses are C_4 plants (mean δ^{13}C value: −11.4‰). In both Kattinkar and Chandemane forest, δ^{13}C of the tree leaves is close to −31.5‰ (±0.4‰) and most of the litter compartments are slightly ^{13}C-enriched (values around −29.7‰). The classical opposition in isotopic composition between C_3 and C_4 plants is thus confirmed at Kattinkar.

In Chandemane, the forest profile is characteristic: the ^{13}C isotopic composition of SOM in the surface horizon is −27‰ and the value increases by 4‰ with depth while the organic carbon content decreases abruptly (Fig. 1) but continuously, without any evidence of an organic paleo horizon. This organic carbon pattern variation with depth is identical for all studied soil profiles (both in Chandemane and Kattinkar). In the toposequence at Kattinkar, the δ^{13}C values of SOM (Fig. 2) of the uppermost part of the soil profiles are very similar to those of the current vegetation, i.e. around −28‰ in profiles 1 and 2 located in forest (as at Chandemane: Fig. 1, and profile F on Fig. 2), and around −13‰ in profile 5 located under savanna (Fig. 1). Profile 3, located at the edge of the forest, presents, in the surface horizon, an intermediate value, near −18‰.

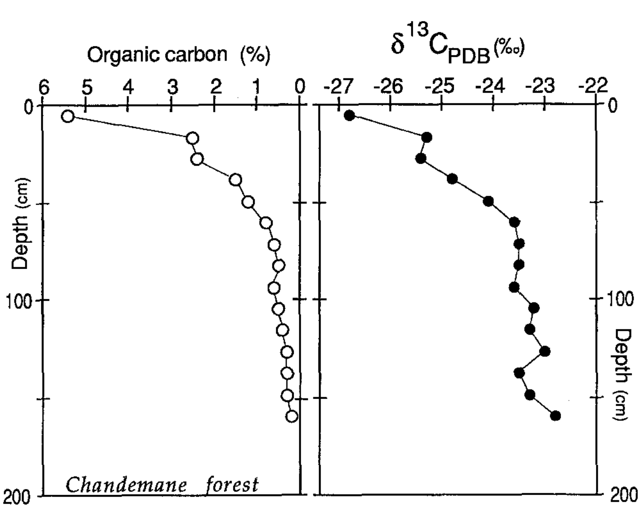

Fig. 1 δ^{13}C values and soil organic carbon content in the evergreen forest in Chandemane

At deeper depths, the classical pattern of a limited ^{13}C enrichment (as observed in Chandemane) is not found in Kattinkar. Under forest (profiles 1 and 2, Fig. 2), the δ^{13}C values of SOM at depth reach −14‰, especially in profile 2: this value is characteristic of organic matter originating from C_4 plants. Therefore, δ^{13}C values of these soils at Kattinkar indicate that areas now dominated by forest (C_3) were once savanna (C_4).

The plot of the δ^{13}C isovalues on this toposequence (with rough limits, according to the small number of profiles) in Fig. 3 enables us to interpret the change of the vegetation from savanna to forest. SOM δ^{13}C values between −17.5 and −20‰, far more ^{13}C-enriched than any δ^{13}C values found in the forest soils of this area (values between −28 and −23‰), can be found more than 100 m inside the forest. Figure 3 thus shows that the forest has recently encroached on savanna. Botanical and ecological observations are consistent with our conclusions (Puyravaud et al. 1994).

Under present savanna vegetation, the deepest part of the profiles (below 50 cm in profile 4, below 100 cm in

Fig. 2 $\delta^{13}C$ values of forest and savanna soils. *F* is the forest profile in Chandemane. In Kattinkar, the profiles are numbered from 1 to 5 along the studied toposequence: 1 and 2 are located under forest, 3 is on the ecotone, 4 and 5 are in the savanna (*cf.* Fig. 3)

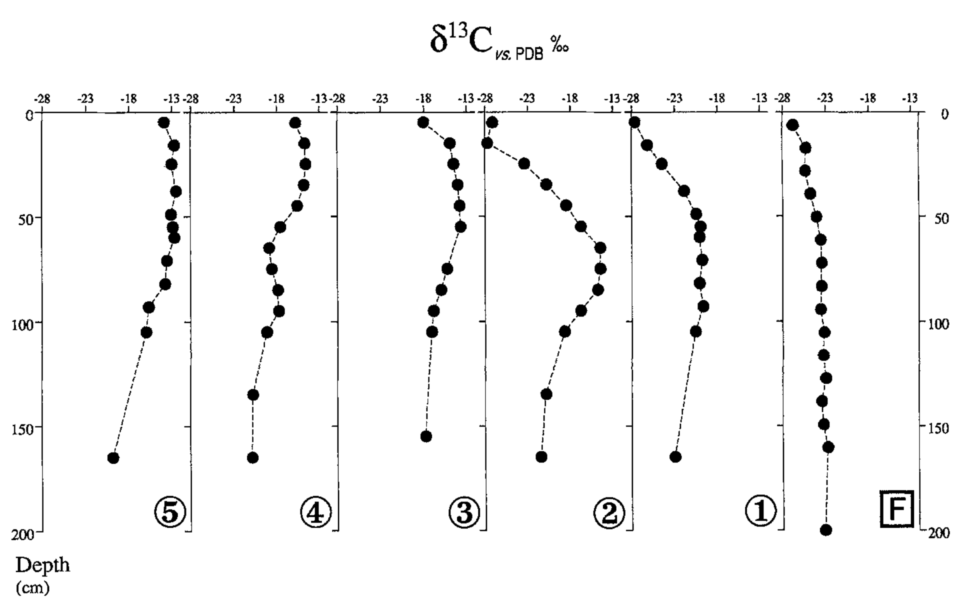

Fig. 3 *SOM* (soil organic matter) $\delta^{13}C$ variations (plot of $\delta^{13}C$ isovalues) along the savanna-forest toposequence in Kattinkar

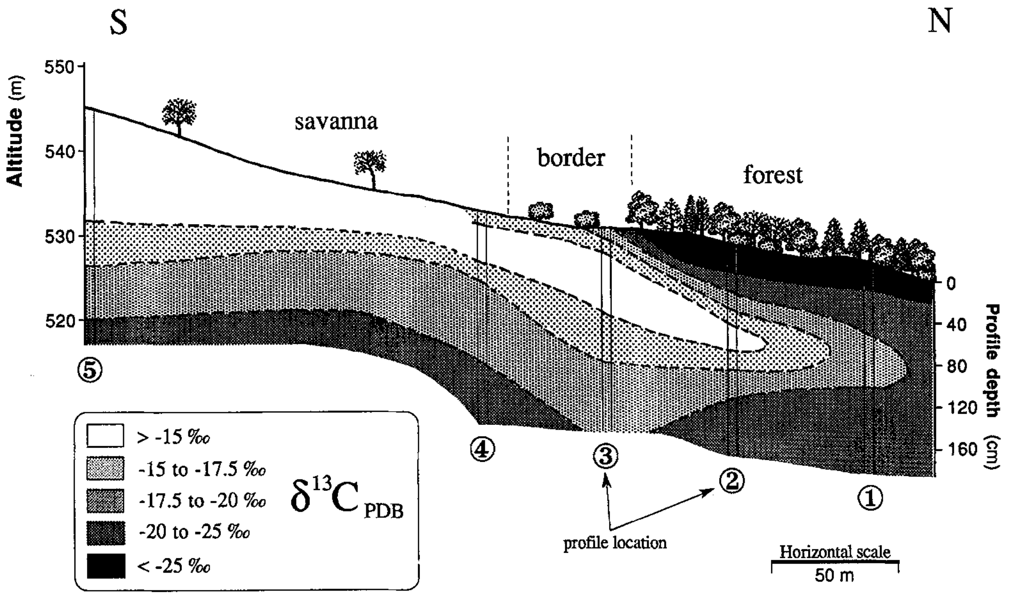

Table 3 Apparent radiocarbon age at different depths on forest profile 2 (Kattinkar, *cf.* Fig. 3)

Sampling depth	Apparent radiocarbon age BP
10–20 cm	Modern
30–40 cm	215 ± 70
50–60 cm	1270 ± 90
80–90 cm	2100 ± 70
130–140 cm	1830 ± 70

profile 5) present very low $\delta^{13}C$ values (less than $-20‰$). Could these low $\delta^{13}C$ values, found at depth in the present savanna soils, possibly represent an earlier savanna phase in which the woody plant component was more important? Such a distribution of the SOM isotopic composition, almost identical to values found at depth under forest at Chandemane, provides justification for our suggestion regarding the preservation of ancient SOM originating from a forest which was present before deforestation and cultivation. It must be pointed out that all savanna-established ecosystems described so far reveal old C_3-derived SOM in deep horizons (Volkoff and Cerri 1987; Martin et al. 1990; Trouvé et al. 1993).

From this study, we can conclude that the creation of savanna, most probably of anthropic origin in this case, is not an irreversible process, although soils have been degraded and impoverished (loss of clays and SOM) after the forest's clearance.

Radiocarbon dates of bulk SOM were performed at Kattinkar in forest profile 2, at depths ranging from 0.10 to 1.40 m (Table 3), and led to apparent radiocarbon ages ranging from 'modern' for surface samples to roughly 2000 BP for deeper samples.

This verifies that older organic matter is located deeper in the profile, and explains the absence of accumulation on these soils. Since the presence of recent C_4 carbon in the 0.80–0.90 m layer is attested by $\delta^{13}C$ values, it can be concluded that the age of old C_3-derived carbon is equal to, or older than, roughly 2000 BP.

This example shows how relevant and powerful the study of SOM ^{13}C content is when investigating recent natural or anthropogenic changes in ecosystem boundaries, in tropical or subtropical areas.

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