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AGRICULTURAL CHEMISTRY AND SOIL FERTILITY

Effect of Soil Carbohydrates on Nutrient Availability in Natural Forests and Cultivated Lands in Sri Lanka[1]

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Abstract—Carbohydrates supply carbon sources for microbial activities that contribute to mineral nutrient production in soil. Their role on soil nutrient availability has not yet been properly elucidated. This was studied in forests and cultivated lands in Sri Lanka. Soil organic matter (SOM) fractions affecting carbohydrate availability were also determined. Soil litter contributed to sugars of plant origin (SPO) in croplands. The negative relationship found between clay bound organic matter (CBO) and glucose indicates higher SOM fixation in clay that lower its availability in cultivated lands. In forests, negative relationships between litter and sugars of microbial origin (SMO) showed that litter fuelled microbes to produce sugars. Fucose and glucose increased the availability of Cu, Zn and Mn in forests. Xylose increased Ca availability in cultivated lands. Arabinose, the main carbon source of soil respiration reduced the P availability. This study showed soil carbohydrates and their relationships with mineral nutrients could provide vital information on the availability of limiting nutrients in tropical ecosystems.

Keywords: Soil organic matter, soil carbohydrates, soil nutrients, forests, cultivated lands

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INTRODUCTION

Carbohydrates constitute 5 to 25% of the organic matter in most soils [8]. Their significance largely stems from the ability of complex polysaccharides to bind inorganic soil particles into stable aggregates [14]. They also form complexes with metal ions, and serve as building blocks for humus synthesis [14, 28]. Other soil properties influenced by carbohydrates include cation exchange capacity (attributed to –COOH groups of uronic acids), and biological activity (energy source for microorganisms) [18, 44].

Carbohydrates are degraded by microorganisms to metabolizable substances, which are the most readily available food for soil organisms [16]. Plant-derived sugars, especially pentose polymers (arabinose and xylose) serve as the major source of energy and C for soil microorganisms. In turn, the microorganisms synthesize primarily hexose polymers (e.g., galactose, mannose, fucose, rhamnose) and release them into the soil [8, 22, 23]. Guggenberger [10] and Amelung [4] showed that plant-derived sugars were concentrated in sand-sized particulate organic matter whereas microbe-derived carbohydrates are accumulated in the clay fraction. Alekseev [2] studied the possibilities of interaction of natural carbohydrates (mono–, oligo–, and poly–saccharides, amino sugars, and natural organic acids of carbohydrate origin) with metal cations and explained that the structural diversity of carbohydrate-metal complexes was caused mainly by their action as ligands. These metal complexes could play an important role in soil nutrient availability. However, these are complicated possibilities, which have not been thoroughly investigated.

Land use changes result in significant decreases in soil carbohydrates due to enhanced mineralization attributed to increased tillage and decreased organic matter inputs [27]. The decreased inputs are also associated with shifts in organic matter quality to more resistant fractions such as clay bound organic forms as more labile pools are decomposed [27]. Soils high in clay and silt are generally higher in SOM than sandy soils, which are attributable to the binding of humus to clay particles, protecting them from further decomposition [19]. Hassink [11] reported that SOM associated with the clay fraction is better protected against decomposition compared to the silt fraction. The CBO is also resistant to the oxidative treatment by interaction with soil minerals [21]. Thus, CBO constitutes an important component in agricultural soils.

Litter particles in the soil constitute another important component in the carbohydrate dynamics. Soil litter has a wide range in its particle sizes. Soil-litter has been defined as the 'light fraction' organic material which passes a 2 mm, but not a 0.25 mm sieve [5]. It consists of particles which are only slightly

[1] The article is published in the original.

Abbreviations: Soil organic matter (SOM), sugars of plant origin (SPO), clay bound organic matter (CBO), sugars of microbial origin (SMO), soil litter (FSL).

Table 1. Descriptive information of the field sites studied

Ecosystem	ELE (m)	MAR (mm)	MAT (°C)	Soil				
				Great group, FAO, 1993	pH	Organic matter, g × 100 g^{-1}	Total N, g × 100 g^{-1}	Total P, g × 100 g^{-1}
Forests								
Tropical wet evergreen, WL	1000	5000	25	Haplic Acrisols	4.57	4.05	0.27	0.04
Tropical semi evergreen, IM	700	2500	24.8	Cambisols	6.13	4.10	0.16	0.05
Moist monsoon, IU	1300	2500	22	Chromic Luvisols	6.98	4.79	0.23	0.04
Dry monsoon, IL	221	2000	27.4	Haplic Acrisols	6.08	2.79	0.11	0.01
Montane, WU	2000	2500	15	Haplic Acrisols	5.74	7.26	0.37	0.04
Dry mixed evergreen, DL	300	1400	28.4	Chromic Luvisols	6.87	1.59	0.23	0.05
Tropical wet evergreen, WM	600	3000	20	Rhodic Nitisols	6.37	3.58	0.29	0.05
Cultivated lands								
Rubber tree, WL	1000	5000	25	Haplic Acrisols	4.63	3.30	0.19	0.05
Export agricultural crops, IM	700	2500	24.8	Cambisols	5.64	2.07	0.07	0.06
Potato farm, IU	1300	2500	22	Chromic Luvisols	6.07	3.78	0.22	0.06
Coconut, IL	221	2000	27.4	Haplic Acrisols	5.19	2.19	0.11	0.03
Tea, WU	2000	2500	15	Haplic Acrisols	5.06	3.56	0.05	0.07
Chena cultivation, DL	300	1400	28.4	Chromic Luvisols	6.71	1.42	0.16	0.04
Home garden, WM	600	3000	20	Rhodic Nitisols	6.00	2.78	0.17	0.06

Note: ELE, Elevation; MAR, Mean annual rainfall; MAT, Mean annual temperature; Climatic regions: WL, Wet zone low country; IM, Intermediate zone mid country; IU, Intermediate zone up country; IL, Intermediate zone low country; WU, Wet zone up country; DL, dry zone low country; WM, Wet zone mid country.

transformed by decomposition. From a study by using scanning electron microscopy, Wattel-Koekkoek [41] reported that CBO fraction indicated free plant remains. Thus, soil litter material serves as an important source for long-term supply of nutrients [40]. Humic substances, CBO and soil litter establish the entire pool of organic matter which could be important in determining the availability of carbohydrates in soil.

Carbohydrates have an important role on SOM dynamics in tropical soils and some studies have been done on this [1, 16, 24, 25, 29, 44]. Most of them are restricted to study their composition and dynamics under different land uses. No attention has been paid to study the effect of the concentration of soil carbohydrates on nutrient availability.

OBJECTS

In this study it is hypothesized that carbohydrates play an important role in governing soil nutrient availability. Limitations of soil carbohydrates are known to constrain mineralization and hence nutrient availability [8]. Also it is hypothesized that different SOM fractions govern the availability of carbohydrates. Therefore in this study soil carbohydrate content and their effects on soil nutrient availabilities were evaluated in forests and adjacent cultivated lands with a view to understand their existing relationships in natural and managed ecosystems. The SOM fractions and their contribution to the availability of soil carbohydrates were also investigated.

MATERIALS AND METHODS

Field Sites

Study sites were located in the main climatic regions of Sri Lanka (5°54′ N—9°52′ N latitude and 79°39′ E—81°53′ E longitude). Descriptive information of the field sites is given in Table 1. In each location, two sites were selected; a natural forest and an adjacent, cultivated land. The natural forests included were tropical wet evergreen (2 forests), semi evergreen, moist monsoon, dry monsoon, montane and dry mixed evergreen forests. Cultivated lands were plantations of 10 year old tea, 20 year old rubber, 40 year old coconut and 25 year old export agricultural crops (pepper, cardamom and cacao), potato, home garden and chena (slash and burn vegetable cultivation). The gardens in turn are surrounded by forests, parts of which were temporarily cleared for slash-and-burn cultivation.

Table 2. Concentrations of soil carbohydrates in different land uses studied

Ecosystem	Sugars of plant origin, SPO		Sugars of microbial origin, SMO					
	Arabinose	Xylose	Rhamnose	Fucose	Ribose	Manose	Galactose	Glucose
	ng g soil^{-1}							
Forests								
Tropical wet evergreen	2.69^{b}	3.52^{b}	5.83^{b}	1.99^{b}	4.24^{b}	4.63^{b}	38.06^{b}	ND
Tropical semi evergreen	ND	1.44^{b}	3.44^{b}	0.93^{b}	3.20^{b}	6.96^{b}	ND	ND
Moist monsoon	14.25^{b}	2.24^{b}	32.13^{a}	598^{a}	182^{a}	374^{a}	1818^{a}	911^{a}
Dry monsoon	96.65^{a}	22.2^{a}	5.76^{b}	12.27^{b}	50.3^{b}	33.03^{b}	92.52^{b}	19.58^{b}
Montane	1.98^{b}	8.69^{b}	3.52^{b}	20.57^{b}	13.44^{b}	19.94^{b}	22.82^{b}	7.52^{b}
Dry mixed evergreen	2.86^{b}	17.15^{a}	5.44^{b}	27.16^{b}	18.29^{b}	9.63^{b}	0.44^{b}	1.14^{b}
Tropical wet evergreen	4.82^{b}	2.63^{b}	6.04^{b}	2.30^{b}	16.21^{b}	2.88^{b}	0.48^{b}	7.44^{b}
CV (%)	114	124	71	78	68	81	128	133
Cultivated lands								
Rubber tree	10.23^{a}	7.58^{a}	48.86^{a}	34.64^{a}	42.5^{a}	26.0^{c}	ND	31.65^{a}
Export agricultural crops	1.45^{b}	ND	1.99^{e}	ND	ND	ND	ND	5.68^{b}
Potato farm	ND	ND	5.95^{c}	7.95^{c}	1.03^{c}	37.6^{b}	130^{a}	ND
Coconut	14.98^{a}	22.19^{a}	36.45^{b}	1.69^{d}	29.40^{b}	51.28^{a}	57.79^{b}	7.79^{b}
Tea	0.192^{d}	1.42^{b}	1.75^{e}	0.49^{e}	ND	1.41^{d}	0.12^{c}	ND
Chena cultivation	1.18^{b}	5.54^{b}	4.25^{c}	12.41^{b}	17.52^{b}	3.04^{d}	ND	1.94^{c}
Home garden	0.534^{e}	21.24^{a}	3.17^{d}	0.98^{e}	16.14^{b}	ND	ND	2.5^{c}
CV (%)	89	47	36	66	89	94	178	138

Note: Values in the same column followed by the same letter are not significantly different at $P < 0.05$. ND, not detected.

Soil Sampling and Analysis

Twenty composited soil samples were collected from 0–20 cm depth at each site, dried and sieved (2 mm). Soils were then ground and sieved (<0.15 mm) prior to the analysis. Macronutrients extracted by modified Morgan extractant [20] and DTPA extractable micronutrients [35] were analysed using an atomic absorption spectrophotometer (GBC 933 AA). Soil PO_4^{3-} (molybdenum blue method [40]) and organic C content (colorimetry [6]) were also measured. The soil was extracted for fulvic fraction and humic acid type substances using the International Humic Substances Society method (IHSS) [36].

Extraction of Clay Bound Organic Matter (CBO)

The separation of clay was done by sedimentation method [39]. Free organic matter in the soil sample (40 g) was first removed by treating with 30% H_2O_2. The amount of CBO in the separated clay fraction was quantified by using weight loss on ignition method.

Extraction of Soil Litter

A sample of soil (100 g) was also extracted to obtain the soil litter for the analysis using the method described by Smucker [32]. The soil sample was agitated in water to separate soil particles and soil litter particles. Organic matter in suspension was carefully decanted onto a 0.25 mm sieve. Soil litter materials collected on the sieve were washed with distilled water and oven dried at 85°C.

Determination of Soil Carbohydrates [3]

Individual sugars were released from soil carbohydrates by treatment with 4M trifluoroacetic acid, the extractant at 105°C for 4 h. The resulting monosaccharides were then converted into alditols acetate derivatives by using acetylation as derivatisation procedure. Reference alditol acetates of rhamnose, fucose, ribose, arabinose, xylose, mannose, galactose, and glucose were used as standards. These derivatives were then separated on a Shimadzu GC–9AM gas chromatograph equipped with a hydrogen flame ionization detector. Separation of the monosaccharide units was achieved with a SPB 1701 fused silica capil-

Table 3. Magnitudes of soil organic matter (SOM) fractions of the natural forests and the adjacent cultivated lands

Ecosystem	Free soil litter, FSL	Clay bound organic matter, CBO
	$g \times 100\ g^{-1}$	
Tropical wet evergreen	0.96 (0.15)	1.02 (0.41)
Rubber tree	0.41 (0.08)	1.67 (0.21)
Difference	0.55*	0.68
Semi evergreen	1.3 (0.07)	1.46 (0.02)
Export agricultural crops	0.54 (0.09)	1.96 (0.12)
Difference	0.76**	0.5**
Moist monsoon	1.14 (0.1)	1.15 (0.09)
Potato farm	0.33 (0.05)	1.18 (0.1)
Difference	0.81**	0.04
Dry monsoon	1.19 (0.27)	0.65 (0.06)
Coconut	0.47 (0.06)	0.68 (0.06)
Difference	1.29**	0.01
Montane	0.64 (0.61)	0.63 (0.03)
Tea	0.29 (0.06)	2.10 (0.66)
Difference	0.35*	1.47
Dry mixed evergreen	0.62 (0.11)	0.77 (0.1)
Chena cultivation	0.28 (0.03)	0.83 (0.03)
Difference	0.34*	0.04

Note: Values within parentheses are standard errors. ** significant at $P < 0.01$, * significant at $P < 0.05$

lary column. Carrier gas was Helium with a total flow rate of 80 mL min^{-1}.

Statistical Analysis

The relationships between concentrations of different sugars and SOM fractions as well as elemental concentrations were established through correlation and regression analyses [30]. The comparison of carbohydrates among different land uses was done using GLM procedure and Tukey's HSD test [30]. A t-test was carried out to compare SOM fractions between the natural forests and the adjacent cultivated lands. Sugar concentrations were transformed to logarithmic scale $[\log_{10}(x + 1)]$.

RESULTS

Table 2 shows the concentration of sugars of plant and microbial origin in the different land uses. The SMO were detected in most of the forest types and they showed a similar pattern among the forest types. Unlike the forests, sugar quantities in cultivated lands were highly variable among sites. Rhamnose showed the highest variation (1.75–48.80 ng g $soil^{-1}$) among the sites. Arabinose and xylose, the SPO were significantly high in rubber (10.23 and 7.58 ng g $soil^{-1}$, respectively) and coconut (14.98 and 22.19 ng g $soil^{-1}$, respectively) plantations, and xylose was high in home garden (21.24 ng g $soil^{-1}$). The SMO were generally low in cultivated lands. They varied between 0.12 ng g $soil^{-1}$ and 37.6 ng g $soil^{-1}$, except 130 ng g $soil^{-1}$ galactose in potato land. However, they were comparatively high in rubber (26.0–48.8 ng g $soil^{-1}$) and coconut (1.69–51.28 ng g $soil^{-1}$) plantations. The lowest concentration of microbial sugars was found in tea soil (i.e.1.75 ng g $soil^{-1}$) and Ribose and glucose were not detected.

Soil litter contents were significantly high in all forests compared to the adjacent cultivated lands (Table 3). The CBO fraction showed a variation among field sites (Table 3). It was high in most of the cultivated lands compared to the forests.

Exchangeable Cu and Zn in the soils of the forests were positively related to the soil fucose contents (Fig. 1a). The exchangeable Mn content was positively related to the soil glucose content (Fig. 1b). Other nutrients did not show significant relationships with the sugars ($P > 0.05$). The soil litter content was negatively related to rhamnose, fucose, ribose and mannose (Fig. 2).

In the cultivated soils, exchangeable Ca was positively related to the xylose content (Fig. 3a) and exchangeable P was negatively related to the arabinose content (Fig. 3b). The soil litter of the cultivated lands was positively related to the soil arabinose and xylose contents (Fig. 4a). The CBO fraction showed a negative relationship to the soil glucose content (Fig. 4b). Humic substances did not show significant relationships with the sugars ($P > 0.05$).

DISCUSSION

The observed differences in soil sugars between forests and the adjacent cultivated lands at each location were mainly due to differences in litter inputs. Soil disturbances due to different management practices of cultivated lands widen the differences in soil carbohydrates among the sites [33]. Low biomass return reduces the concentration of carbohydrates in tea soils. The heavy use of agrochemicals reduces the decomposition processes by lowering the microbial activities, which in turn reduce the concentration of CMO as observed in tea soils. However, there was a lesser deviation among the concentrations of sugar types in the forests as there were no such soil disturbances. This further shows that carbohydrates are sensitive parameters and useful in detecting land use changes [13].

Positive relationships between soil litter and SPO (arabinose and xylose) indicated that soil litter is the major source of the sugars in the cultivated lands [8, 18, 28]. In the cultivated lands direct litter incorporation into the soil with management– induced mixing, generally enhances the amount of SPO [33]. However, in the forests, carbohydrates are depleted due to mineralization processes during litter humification [10]

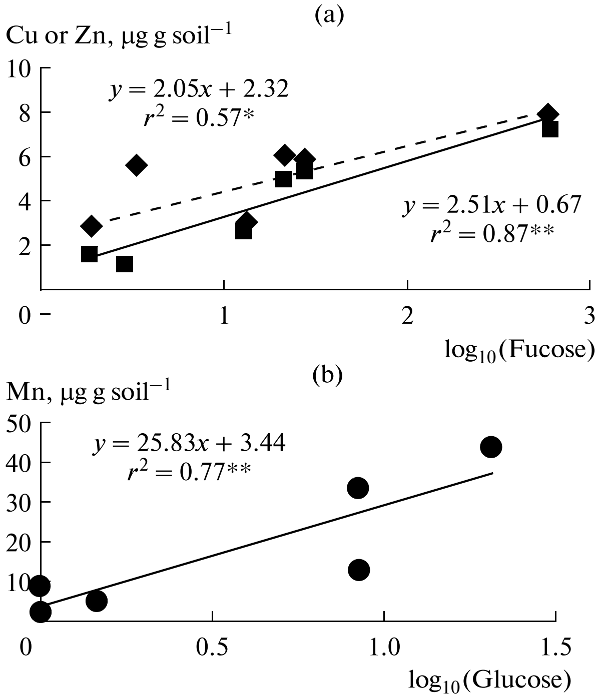

Fig. 1. Relationships between soil carbohydrates and nutrients. (a) Exchangeable Zn (◆---) and Cu (—■) versus fucose (b) Exchangeable Mn versus glucose, in 7 major forest types (tropical wet evergreen (2 forests), semi evergreen, moist monsoon, dry monsoon, montane and dry mixed evergreen). Each data point in the figure represents a mean of 20 composite soil samples per site. ** significant at $P < 0.01$, * significant at $P < 0.05$.

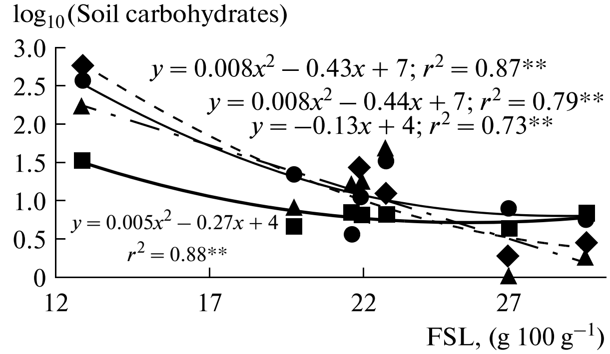

Fig. 2. Relationships between soil litter content (FSL) and soil carbohydrates. Rhamnose (—■), fucose (◆---), ribose (—▲) and mannose (—●) in 7 major forest types [tropical wet evergreen (2 forests), semi evergreen, moist monsoon, dry monsoon, montane and dry mixed evergreen]. Each data point in the figure represents a mean of 20 composite soil samples per site. ** significant at $P <$ 0.01, * significant at $P < 0.05$.

with high microbial activities compared to the cultivated lands. These processes reduce the amount of SPO in the forests. Therefore, the dominant sugars in the forests are microbial in origin. This was reflected in the present study by the relationships in the forest soils with SMO. Further, the negative relationships between soil litter and the SMO (rhamnose, fucose, mannose, ribose) indicated exploitation of the sugars as energy sources by litter decomposing microorganisms, because it has been shown that when there is a high soil litter content, microbial respiration could also be high in forest ecosystems [37, 38].

The negative relationship between CBO and glucose content indicates that higher the SOM incorporation to clay, lower the availability of soil glucose in cultivated lands. This may be due to the fact that once the SOM was encapsulated within clay particles forming CBO [31], they could not further release their sugars.

In the forests, fucose and glucose increased the availability of Cu, Zn and Mn by enhanced mineralization processes possibly due to high substrate utilization and oxygen consumption. It is reported that the addition of glucose enhanced the growth of white rot fungi in soil via increased secretion of Mn peroxidase enzyme which breaks down lignin [43]. This implies the possible relationship between glucose and soil Mn that was observed in our results. In addition, the sugars increased the availability of micronutrients probably by forming soluble complexes with micronutrients [17]. It has been suggested that microbial release of simple carbohydrate molecules with chelating properties can accelerate chemical weathering and consequently nutrients release [17].

In general, it is reported that the nutrient availability is increased by sugars [8, 13, 18, 25, 42]. However, microbially derived sugars may be stabilized by interaction with soil minerals, limiting their availability [15]. It therefore seems that in the forests the SMO (fucose and glucose) are the major monosaccharides that limit nutrient availability, especially micronutrients.

In the cultivated lands the SPO (xylose and arabinose) governed nutrient availability. Xylose increased the availability of Ca probably by reducing Ca fixation [17]. Sugars are generally expected to increase the availability of cations by coating clay particles forming amino sugar compounds and preventing fixation [13, 34]. Arabinose reduced the available P content in the soil. This may be due to heavy utilization of P in the presence of arabinose, which is reported to be major carbon source for soil respiration [7].

The results showed that there was a higher contribution of SMO to the nutrient availability in the forest, as their availability is high compared to the SPO [15]. Sugars act as a source of energy for microbes, supporting nutrient mineralization in C limiting tropical soils. Solomon [33] reported that the clay fraction is enriched with microbially derived carbohydrates whereas coarse and fine sand fractions of soil are enriched with plant-derived carbohydrates. Since the dominant sugars in the forest soils are microbial in origin, which are associated with clay, the fine soil fraction would be the most suitable fraction to study the

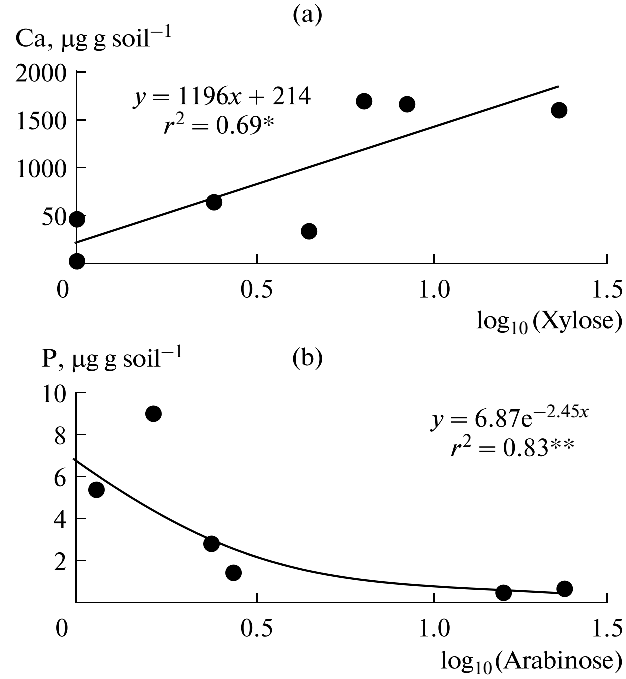

Fig. 3. Relationships between soil carbohydrates and nutrients. (a) Exchangeable Ca versus xylose, (b) exchangeable P versus arabinose, in 7 major cultivated lands (tea, rubber, coconut, export agricultural crops, home garden, potato and chena). Each data point in the figure represents a mean of 20 composite soil samples per site. ** significant at $P < 0.01$, * significant at $P < 0.05$.

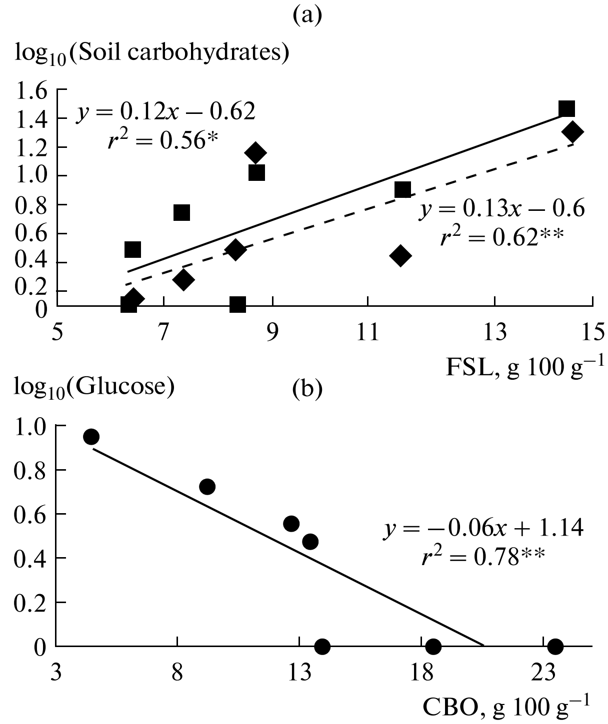

Fig. 4. Relationships between (a) soil litter content, and arabinose (—◆) and xylose (---■), (b) clay bound organic matter (CBO) and glucose, in 7 major cultivated lands (tea, rubber, coconut, export agricultural crops, home garden, potato and chena). Each data point in the figure represents a mean of 20 composite soil samples per site. ** significant at $P < 0.01$, * significant at $P < 0.05$.

existing relationships. In this fraction, all microbially derived sugars are concentrated in the clay particles. In contrast, in the cultivated lands the nutrient availability is determined by the plant derived sugars. Correlations found in the study confirm that the effect of the SOM on the availability of nutrients is through the effects of soil carbohydrates under these tropical climatic conditions. As many other organic substances, sugars also can serve as chelates for micronutrient metals [26]. Chelates are soluble organic compounds that bind metals such as Cu, Fe, Mn, and Zn, and increase their solubility and availability to plants [9, 12]. In our study, the correlations observed between sugars and the micronutrients could possibly be due to this.

CONCLUSIONS

The study confirmed that in the forests there was a greater influence of SMO to nutrient availability, while in the cultivated lands the nutrient availability was determined by SPO. Soil litter was the major source of sugars in both ecosystems. In the cultivated lands, soil litter enhanced the sugar availability whereas in the forests soil litter decreased it by altering microbial activities. Thus, soil litter is an important indicator of soil quality in terms of soil carbohydrate and nutrient availability. The effect of the SOM on the availability of nutrients was found to be through the effects of soil carbohydrates in these tropical climatic conditions. Therefore, soil carbohydrates and their relationships with soil nutrients in different land use practices may provide vital information regarding the availability of limiting nutrients in natural and managed ecosystems in the tropics. This is the first study of this nature in which, relationships among SOM fractions, soil carbohydrates and nutrients have been established. Further experiments that directly evaluate carbohydrate controls over nutrient cations are however needed to fully understand the mechanisms behind these relationships.

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