

Spatial variation of soil respiration across a topographic gradient in a tropical rain forest in French Guiana

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Abstract: The objective of this study was to analyse the factors explaining spatial variation in soil respiration over topographic transects in a tropical rain forest of French Guiana. The soil of 30 plots along six transects was characterized. The appearance of the 'dry to the touch' character at a depth of less than 1.2 m was used to discriminate soils exhibiting vertical drainage from soils exhibiting superficial lateral drainage and along with colour and texture, to define five classes from well-drained to strongly hydromorphic soils. Spatial variation in soil respiration was closely related to topographic position and soil type. Increasing soil water content and bulk density and decreasing root biomass and soil carbon content explained most of the decrease in soil respiration from the plateaux (vertically drained hypoferralic Acrisol) to the bottomlands (haplic Gleysol). These results will help to stratify further field experiments and to identify the underlying determinants of spatial variation in soil respiration to develop mechanistic models of soil respiration.

Key Words: Acrisol, carbon balance, carbon flux, Gleysol, root biomass

INTRODUCTION

Above-canopy eddy covariance measurements of CO₂ fluxes, large-scale analyses of ¹³C signatures of atmospheric CO₂, and biomass inventories have all highlighted a putative carbon sink in neotropical forests that might counterbalance deforestation (Ciais *et al.* 1995, Grace *et al.* 1995, Malhi & Grace 2000, Malhi *et al.* 1999, Miranda *et al.* 1997, Williams *et al.* 1998). Carbon sequestration in forest ecosystems often results from a small difference between photosynthetic carbon fixation (gross primary production) and ecosystem respiration (Granier *et al.* 2000, Valentini *et al.* 2000). Soil respiration is one of the main components of ecosystem respiration (Chambers *et al.* 2004, Granier *et al.* 2000, Janssens *et al.* 2001) and this carbon flux component seems very sensitive to climate condition such as seasonal changes in temperature and/or soil water content (Epron *et al.* 1999a, Hanson *et al.* 1993).

Factors that control temporal variation in soil respiration have now been identified in a wide range of forest ecosystems (Davidson *et al.* 1998, Epron *et al.* 1999a, 2004; Hanson *et al.* 1993, Rey *et al.* 2002), while factors explaining spatial variation have been less explored. Spatial variability in soil respiration is known to be very large, especially at small scales. This variability has been related to root biomass, microbial biomass, litter mass, soil organic carbon, soil nitrogen, cation exchange capacity, soil bulk density, soil porosity, soil pH and site topography (Fang *et al.* 1998, Hanson *et al.* 1993, La Scala *et al.* 2000, Rochette *et al.* 1991, Soe & Buchmann 2005, Xu & Qi 2001). These factors may affect all processes that contribute to soil respiration, such as respiration of roots and their associated rhizosphere, and respiration of soil micro-organisms that decompose the organic materials from both above-ground and below-ground litter (Boone *et al.* 1998, Bowden *et al.* 1993, Epron *et al.* 1999b, 2001). Soil respiration data from tropical ecosystems concern mainly secondary forests, plantations or pasture (Epron *et al.* 2004, Janssens *et al.* 1998, Salimon *et al.* 2004). The few studies dealing with undisturbed forest have focused

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on temporal variation in soil respiration (Davidson *et al.* 2000, Doff Sota *et al.* 2004, Hashimoto *et al.* 2004). The influence of soil drainage and topography on soil respiration has scarcely been investigated (Chambers *et al.* 2004).

The Atlantic side of the Guiana Shield in French Guiana provides a good opportunity to study small-scale spatial variation in soil respiration because it is characterized by an undulating topography due to a multitude of small hills and valleys. **Topography generates local microclimate and leads to variation in soil drainage and soil organic matter distribution that can directly influence soil respiration by changes in soil water content or temperature** (Garret & Cox 1973, Hanson *et al.* 1993, Kang *et al.* 2003). Moreover, spatial variation in microclimate or soil drainage may have indirect influences on soil respiration through effects on species composition and plant productivity.

The objectives of this study were to analyse the spatial variation of soil respiration in a 50-ha experimental site in the tropical rain forest of French Guiana characterized by a patchwork of hills and valleys, and to discuss the factors explaining spatial variation in soil respiration over topographical gradients from well-drained to strongly hydromorphic soils.

MATERIALS AND METHODS

Site description

The study site was located in the Paracou experimental forest in French Guiana (**5°15'N, 52°55'W; 0–50 m elevation**), 15 km inland from the coast (Gourlet-Fleury *et al.* 2004). Mean annual precipitation averages 2980 mm (30-y period) with a long dry season (less than 100 mm mo^{-1} rain) from mid-August to mid-November and a short dry season in March. Air humidity and air temperature exhibit little seasonal variation. Mean values of air temperature and daily minimum relative humidity range between 25.7 °C and 70% during the rainy season in May and 26.7 °C and 58% during the dry season in November.

The study site extends over 50 ha of undisturbed forest and is characterized by a patchwork of hills (100–300 m in diameter and 20–50 m high) separated by humid valleys. The floristic composition (trees with dbh \geq 10 cm) is dominated by three families (Lecythidaceae, Caesalpiniaceae and Sapotaceae) that represent respectively 18, 13 and 12% of the total basal area. Leaf area index is close to 7 and average canopy height is 32 m. Soils are mostly **acrisol** (FAO-ISRIC-ISSS 1998) developed over a Precambrian metamorphic formation called the Bonidoro-serie. It is characterized by schists and sandstones and **locally crossed by veins of pegmatite,**

aplite and quartz. **Six topographical transects were established on two hills within the experimental site (three per hill in different directions).** The lengths of these transects ranged between 75 m and 150 m, and differences in altitude between top and bottom ranged between 25 and 35 m. Five plots (2.5 \times 2.0 m) were distributed along each transect. One plot was located at the top of the ridge (or very close to it), one on the upper slope, one on the mid-slope, one on the lower slope, and one in the bottomland.

Soil in each plot was characterized by extracting a 1.2-m core. Soil texture, soil colour (Munsell code), as well as the presence of stones or coloured spots were examined at depths of 0.1 m, 0.2 m and every 0.2 m below, and were used to classify soils. **The depth of the drainage barrier was subjectively localized by manual perception of clay content and silt dryness.** The appearance of the 'dry to the touch' character at a depth of less than 1.2 m was used to discriminate soils exhibiting vertical drainage from soils exhibiting superficial lateral drainage (Boulet *et al.* 1979, Sabatier *et al.* 1997).

An adjacent topographic transect (100 m length, 21 m elevational difference) was used to open a deep trench (1.5 m depth) at each topographic position. Each soil layer was characterized by its texture, colour and clay content. Soil samples were collected with an auger in each soil layer and then air dried at ambient conditions and passed through a 2-mm sieve. Clay content (0–2 μm particle size) was determined gravimetrically by the pipette method after soil organic matter oxidation with H_2O_2 and dispersion with sonication (French standard NF X31-107, AFNOR 1994).

Measurements of soil respiration, temperature and water content

In each plot, soil respiration (SR) was measured at 30 points within a 2.5 \times 2-m matrix with 0.5-m spacing. SR was measured using two identical soil respiration chambers operating in closed mode (SRC-1, PP Systems, UK) modified according to Le Dantec *et al.* (1999), in which the increase of the CO_2 concentration was recorded with an infrared gas analyser (either EGM-1 or CIRAS 1, PP Systems, UK). Cross calibration showed no chamber or analyser effect. The chamber edge was inserted in the soil to a depth of 0.5 cm. The litter overlying the soil was thus included in the chamber during the measurement. The increase in the CO_2 concentration in the chamber was recorded until it reached 50 $\mu\text{mol mol}^{-1}$, or after a maximum delay of 120 s. Measurements were made during a 7-d period in September during which there was no rain. Variation in SR at this temporal scale is very limited, except after strong rainfall (unpublished data, but see also Buchmann *et al.* 1997, Doff Sota *et al.* 2004).

Soil temperature was monitored simultaneously with soil CO₂ efflux using a soil penetration probe (STP-1, PP Systems, UK) inserted in the soil to a depth of 5 cm in the vicinity of the soil respiration chamber. The volumetric soil water content in the topsoil layer (0–6 cm) was monitored with a theta probe (ML2, Delta-T Device Ltd, Cambridge, UK) just after respiration measurement at the chamber location. The probe was cross-calibrated with the gravimetric water content of 170 soil samples collected in the plots as described below.

Roots, litter and soil characteristics

Above-ground litter was collected over half of the plot area (2.5 m²) immediately after respiration measurements. Six soil cores (3.3-cm diameter, 6.0-cm depth) were sampled on a 1 × 2-m matrix with 1-m spacing covering the plot, stored in a plastic bag and weighed. Soil samples were sieved and root fragments (< 5-mm diameter) were washed, oven-dried at 60 °C to constant mass and weighed.

Soil subsamples were then weighed, oven-dried at 105 °C to constant mass and weighed again. Volumetric water content and bulk density were calculated from soil mass and core volume. Soil pH was determined in a 1:2.5 soil:water ratio. The six soil subsamples of each plot were pooled into a composite sample. The concentrations of organic carbon were determined on these 30 composite samples with a total organic carbon analyser (TOC-5050-Shimadzu, Japan).

Data analysis

For each parameter in each plot, the mean value and 95% confidence intervals (CI_{95%}) were calculated. Analyses of variance were conducted to assess the difference in measured parameters between soil types with plots nested within soil type (nested ANOVA). Contrasts were used to test relevant differences between soil types when the overall model was significant.

Correlation analyses were used to examine influences of soil factors (temperature, water content, carbon concentration, soil pH, bulk density, litter mass and root density) on soil respiration. Partial correlation analysis was further used to discard putative confounding effects of one variable on the correlation between soil respiration and another variable.

RESULTS

Soil classification

Soils were classified into five classes depending on drainage conditions. Soils exhibiting vertical drainage (hypoferralic acrisol, four plots, A_{HF}) were observed on

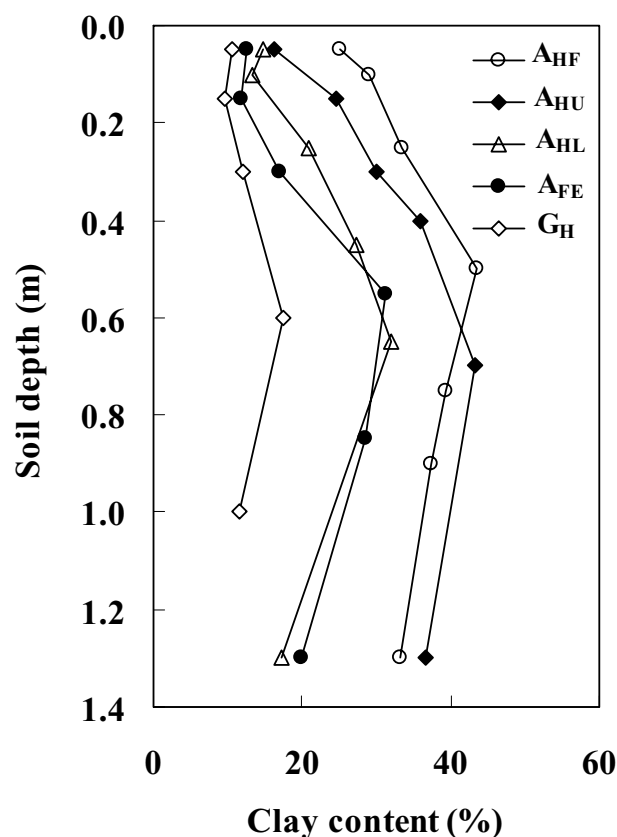


Figure 1. Vertical distribution of clay content in soil profiles in five contrasting soils along one topographic transect in the Paracou experimental forest in French Guiana. Soil types were hypoferralic acrisol (A_{HF}), haplic acrisol on the upper (A_{HU}) or lower (A_{HL}) position, ferric acrisol (A_{FE}) and haplic gleysol (G_H).

the upper parts of hills. The A_{HF} soil profile exhibited the highest clay content in the first 60 cm (Figure 1). Soils with superficial lateral drainage (haplic acrisol) exhibited various depths of the drainage barrier (60–80 cm) that restricted the vertical drainage. They were observed along the slope, either on the upper part of the slope (nine plots, A_{HU}) or in the middle or the lower part (eight plots, A_{HL}). Within a given transect, the depth of this barrier depended on the topographical position of the plot. Deeper barriers were found on the upper part of the slope. A_{HU} and A_{HL} soils profiles exhibited different clay content below the first 5 cm, with lower clay content lower on the slope (Figure 1). Hydromorphic soils, with the water table occasionally in the upper horizon (ferric acrisol, five plots, A_{FE}), were observed on the lower slopes or in the bottomlands. They exhibited red and yellow mottled saprolite at a depth of less than 1.2 m, but the soil profile exhibited similar clay content to the A_{HL} profile (Figure 1). Strongly hydromorphic soils with the water table permanently in the upper horizon (haplic gleysol, four plots, G_H) were found in some bottomlands. This soil profile exhibited the lowest clay content (Figure 1).

Table 1. Summary of the effects of soil type on soil respiration (SR), volumetric soil water content (SWC), bulk density (BD), soil carbon content (SOC), soil pH (pH), root density (RD), soil temperature (ST) and leaf litter mass (LL), as recorded over 30 plots along six topographical transects in the Paracou experimental forest in French Guiana. Soil types were hypoferralic Acrisol on the upper parts of hills (A_{HF}), **haplic Acrisol on the upper (A_{HU}) or lower (A_{HL}) slopes**, ferric Acrisol on the lower slopes or in bottomlands (A_{FE}) and haplic Gleysol (G_H) in some bottomlands. Shown is the F-statistic of nested ANOVA for testing differences between soil types ($df = 4$) and between plots within soil types ($df = 25$). F values significantly higher than 1 were followed by * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ^{NS} means not significant.

	F statistic values		
	Replicates	Soils	Plots
SR	891	39***	6.4***
SWC	891	567***	41***
BD	180	27***	5.4***
pH	180	15***	8.6***
SOC	30	4.7**	–
RD	180	12***	3.5***
ST	891	197***	89***
LL	30	0.3 ^{NS}	–

Soil respiration

The average ($\pm CI_{95\%}$) value of soil respiration was $4.26 \pm 0.13 \mu\text{mol m}^{-2} \text{s}^{-1}$ ($n = 891$). Variability in soil respiration within each plot was quite large, with coefficients of variation ranging between 23% and 73%. Mean soil respiration of the plots ranged between 2.20 and $6.46 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Spatial variability of soil respiration between plots was partly related to soil type along topographic transects (Figure 2a) with a significant decrease in soil respiration from A_{HF} hilltop soils to G_H bottomland soils (nested ANOVA, Table 1). This pattern was associated with lower root density in G_H soils in the bottom of the valleys compared with the other soil types (Figure 2b) and with a decrease in soil carbon content from vertically drained soils to hydromorphic soils (Figure 2c). Soil water content increased with decreasing drainage ability from vertically drained A_{HF} soils to G_H soils, but the difference between ferric Acrisol and haplic Acrisol found in the lower part of the slopes was not significant (Figure 2d). A similar although less-pronounced pattern was observed for bulk density (Figure 2e). Leaf litter mass was not significantly different among soil types (Figure 2f). Despite significant differences, soil pH and soil temperature varied in very narrow ranges (less than 0.2 and 0.8°C respectively, Figures 2g, h).

Relationships between soil respiration and soil characteristics

Among plots, soil respiration was significantly and negatively correlated with soil water content, bulk density

Table 2. Bravais–Pearson correlation coefficients among mean values of soil respiration (SR), volumetric soil water content (SWC), bulk density (BD), soil pH (pH), soil carbon content (SOC), root density (RD), soil temperature (ST) and leaf litter mass (LL), as recorded over 30 plots along six topographical transects in the Paracou experimental forest in French Guiana. Values in bold are significant at $P = 0.05$.

	SWC	BD	pH	SOC	RD	ST	LL
SR	−0.67	−0.71	−0.42	0.70	0.62	0.42	−0.01
SWC		0.47	0.27	−0.62	−0.51	−0.53	0.08
BD			0.29	−0.70	−0.46	−0.46	0.02
pH				−0.45	−0.41	−0.12	−0.02
SOC					0.54	0.57	0.08
RD						0.23	−0.19
ST							0.13

and soil pH (Table 2, Figures 3a–c), and positively related to soil carbon content and root biomass and soil temperature (Figures 3d–f). However, soil temperatures exhibited a very narrow range during the measurement campaign with a mean ($\pm CI_{95\%}$) of $25.60 \pm 0.04^\circ\text{C}$ ($n = 891$). Soil respiration was not correlated with litter mass (data not shown).

Despite a positive correlation between soil water content and bulk density (Table 2), partial correlation analysis discarded strong confounding effects of soil water content on the correlation between soil respiration and bulk density ($r_p = -0.56$). A similar conclusion was drawn about putative confounding effects of soil water content on the correlation between soil respiration and soil carbon content ($r_p = 0.49$) and about the effect of bulk density on the correlation between soil respiration and soil carbon content ($r_p = 0.42$). Partial correlation analysis also discarded strong confounding effects of soil water content, soil carbon content or bulk density on the correlation between soil respiration and root density (r_p of respectively 0.43, 0.40 and 0.44). In contrast, there was a clear confounding effect of either soil carbon content or root biomass on the correlation between soil respiration and soil pH ($r_p = 0.16$ and 0.22 respectively).

DISCUSSION

Mean soil respiration rate ($4.3 \mu\text{mol m}^{-2} \text{s}^{-1}$) in the study site was consistent with those reported for the Amazonian region (Chambers *et al.* 2004, Doff Sotta *et al.* 2004), similar to those observed in Paracou forest by Buchmann *et al.* (1997) during the dry season ($4.7 \mu\text{mol m}^{-2} \text{s}^{-1}$), but higher than those reported by Janssens *et al.* (1998) during the rainy season ($2.3 \mu\text{mol m}^{-2} \text{s}^{-1}$).

The experimental procedure that was used in this study did not provide insight to the cause of the large spatial variability that was observed within some plots. Within a plot, spatial variation of soil respiration was not related to soil water content (data not shown) but it was thought

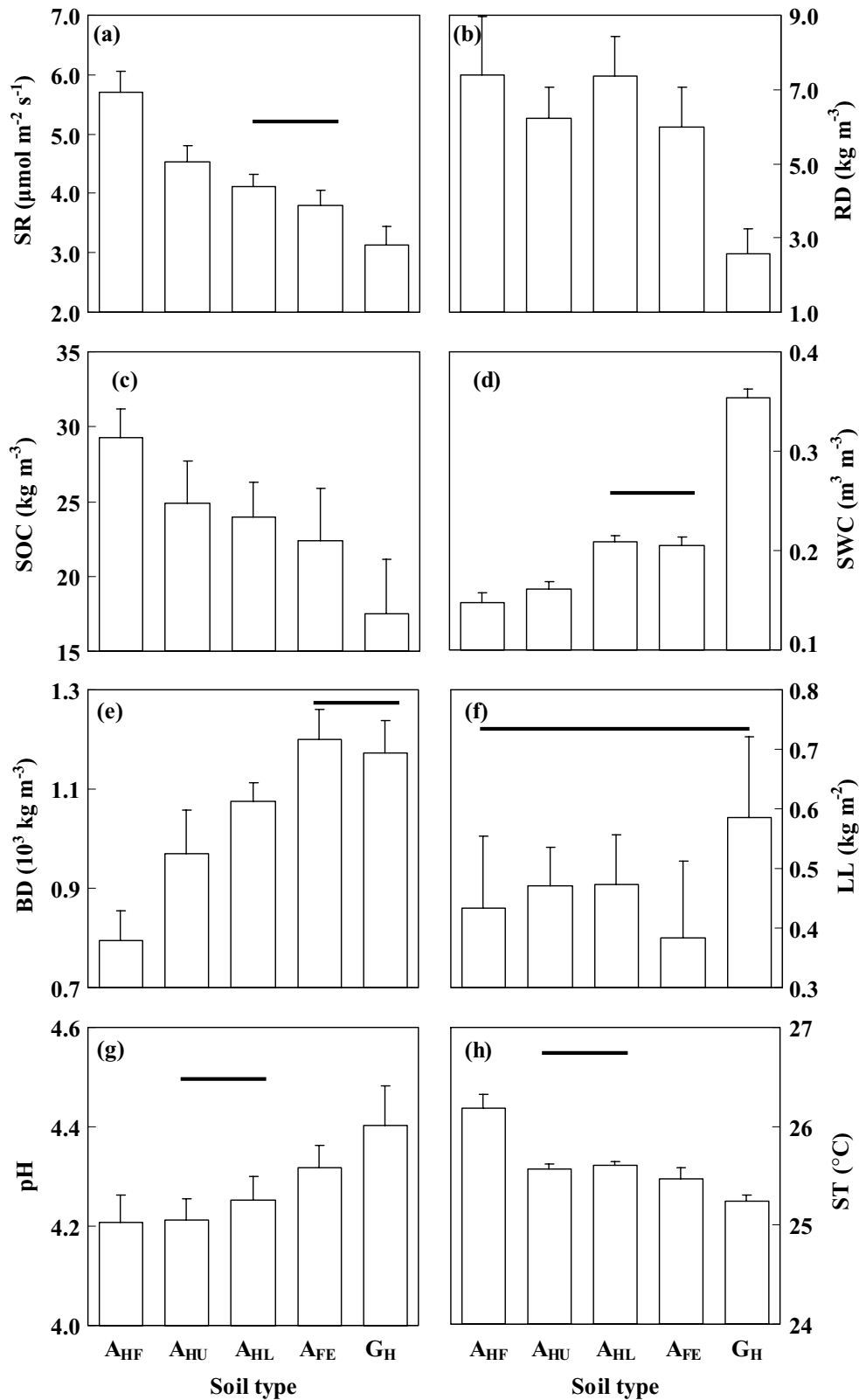


Figure 2. Variation in (a) soil respiration (SR), (b) root density (RD), (c) soil carbon content (SOC), (d) volumetric soil water content (SWC), (e) bulk density (BD), (f) leaf litter mass (LL), (g) soil pH (pH) and (h) soil temperature (ST) with soil types along six topographical transects in the Paracou experimental forest in French Guiana. Soil types were hypoferralic acrisol on the upper parts of hills (A_{HF}), haplic acrisol on the upper (A_{HU}) or lower (A_{HL}) slope, ferric acrisol on the lower slope or in bottomlands (A_{FE}) and haplic gleysol (G_H) in some bottomlands. The difference between two adjacent means covered by a horizontal line is not significant (contrast analysis, $P \geq 0.05$).

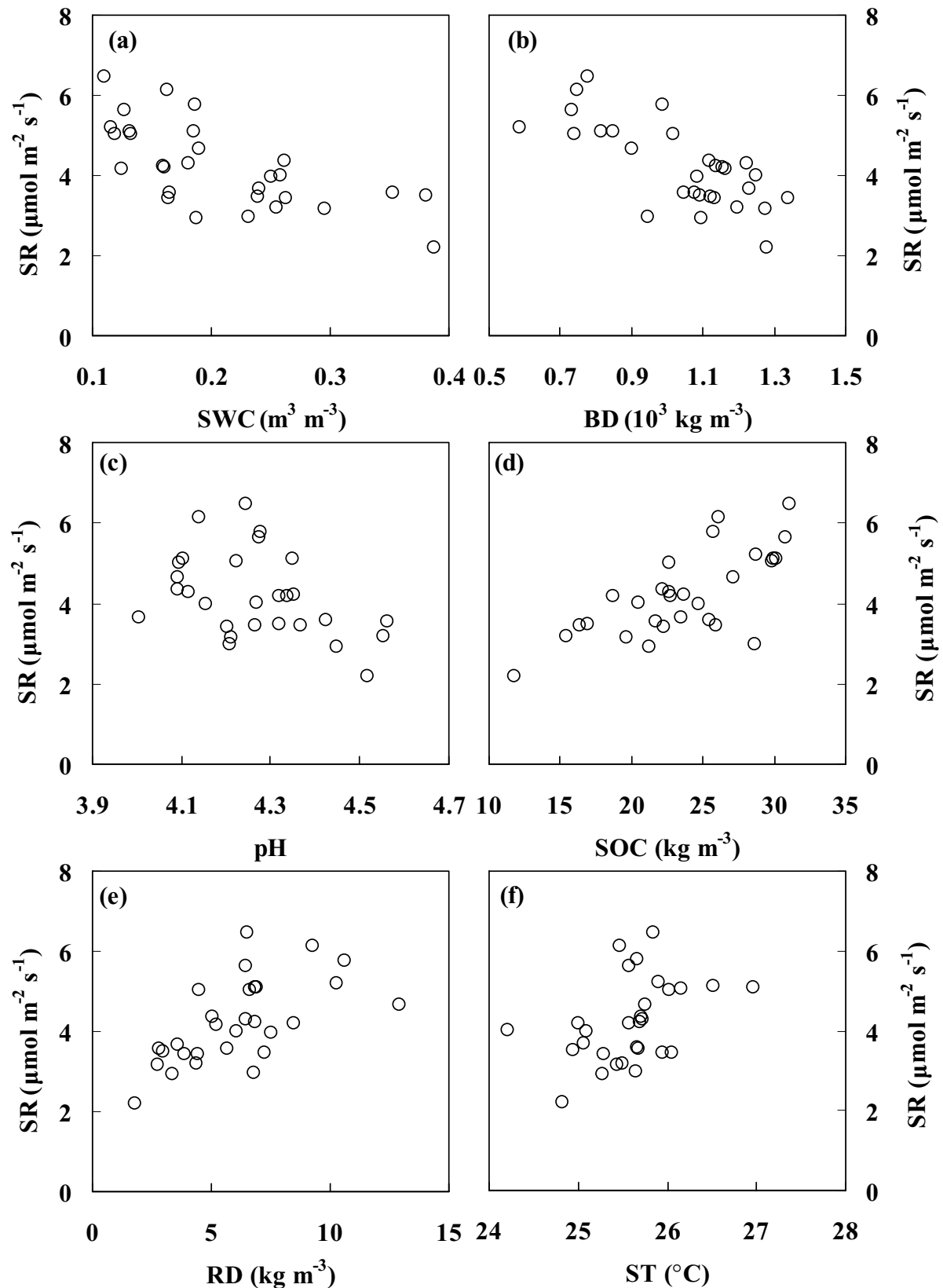


Figure 3. Relationships between mean soil respiration (SR) and (a) volumetric soil water content (SWC), (b) bulk density (BD), (c) soil pH (pH), (d) soil carbon content (SOC), (e) root density (RD) and (f) soil temperature (ST) recorded over 30 plots across the experimental site. Coefficients of correlation between SR and the six variables are shown in Table 2 (first line of the matrix), all of which were significant at $P = 0.05$.

to be due to non-uniform addition of organic detritus, heterogeneous distribution of fine roots, distance to tree or aggregative distribution of soil fauna (Epron *et al.* 2004, Savin *et al.* 2001, Stoyan *et al.* 2000).

At a larger scale, soil respiration varied strongly with topographic position, decreasing from the hilltops (vertically drained hypoferralic acrisol) to bottomlands (haplic gleysol), and a similar pattern to that observed in the Central Amazon (Chambers *et al.* 2004). There is no typical ferralsol exhibiting deep vertical drainage in this site (DVD soils in the French Guiana nomenclature, Sabatier *et al.* 1997). Hypoferralic acrisol (A_{HF}) that are observed on the upper parts of hills exhibited a reddish-brown clayey horizon with a micro-aggregated structure (like ferralsol) followed by a red clayey weathered horizon (alloterite) at a depth of less than 1.2 m (Alt soils in the French Guiana nomenclature, Sabatier *et al.* 1997). Haplic acrisol (A_{HU} and A_{HL}) are soils with superficial lateral drainage (SLD soils in the French Guiana nomenclature, Boulet *et al.* 1979, Guehl 1984, Sabatier *et al.* 1997) that exhibited a drainage barrier at a depth between 60 and 80 cm. This barrier, a dark red silty horizon (isalterite) remains 'dry to the touch' in all seasons. Haplic gleysol (G_H) that are found in some bottomlands exhibited surface hydromorphy (SH soils in the French Guiana nomenclature, Sabatier *et al.* 1997) with a permanent water table in the upper horizon.

Between-plot variability in soil respiration was strongly related to five of the seven tested soil descriptors, i.e. volumetric soil water content, bulk density, soil carbon content, soil pH and root density. The strong negative relationship between soil respiration and soil water content contrasted with previous results that highlighted soil water content controlling temporal but not spatial variation in soil respiration (Epron *et al.* 2004, Xu & Qi 2001). In contrast, soil water content did contribute to spatial patterns of soil respiration in central Korea where slope exposure strongly influences soil water content (Kang *et al.* 2003). Low soil water content often restricts soil respiration (Epron *et al.* 1999a, Epron *et al.* 2004, Rey *et al.* 2002), but high soil water content might limit oxygen diffusion through the soil porosity and therefore microbial activity (Davidson *et al.* 1998, Xu & Qi 2001). High soil water content at the bottom part of the topographic gradients, even during the dry season, could therefore account for lower soil respiration. High bulk density might also limit oxygen diffusion into the soil profile. A similar negative correlation between bulk density and soil respiration has been observed in a ponderosa pine plantation (Xu & Qi 2001). However, since there was a strong negative correlation between bulk density and soil carbon content, the correlation between bulk density and soil respiration might also hide a causal relationship between soil carbon content and

soil respiration. The relationship between soil carbon content and soil respiration is complex since both positive and negative correlations have been reported (Fang *et al.* 1998, Scott-Denton *et al.* 2003, Stoyan *et al.* 2000). A negative correlation is expected when decomposition rates are limited by adverse climatic or edaphic conditions (cold, damp and acidic soil for instance). In contrast, a positive effect of soil organic matter on water retention is thought to account for the positive correlation between soil carbon content and soil respiration in managed agrosystems (Stoyan *et al.* 2000, Tufekcioglu *et al.* 2001). However, this effect is not expected here because both soil respiration and soil carbon content were negatively correlated to soil water content. The observed positive correlation is thought to reflect substrate limitation in this tropical rain forest. More soil organic matter due to higher litter fall and/or dead root production, or more likely due to better retention in the upper soil horizon, provides soil micro-organisms with higher concentration of carbon substrates. High clay content and presence of Al^{3+} at low pH would favour formation of organo-mineral complexes in tropical soils (Feller *et al.* 1991, Greenland *et al.* 1992, Ohta & Effendi 1992, Powers & Schlesinger 2002, Spain 1990). Then, higher clay contents together with lower pH in upslope positions would favour soil organic matter retention in the upper soil layers while lower clay content of hydromorphic soils would favour drainage of organic carbon. Indeed, flow of dissolved organic carbon is thought to be important for the carbon balance of Amazonian forests (Richey *et al.* 2002).

Positive relationships between soil respiration and root density are a common feature in many forest ecosystems (Fang *et al.* 1998). Indeed, many studies have shown that root contribution accounts for about half of soil respiration in forest ecosystems (Epron *et al.* 1999b, Ewel *et al.* 1987, Nakane *et al.* 1996). In addition to the respiration of living roots, microbial activity may also account for the correlation between soil respiration and root density since decaying dead root and root exudates provide carbon substrates to the soil microflora.

The lack of correlation between litter mass and soil respiration despite a large range in litter mass suggests that CO_2 flux from leaf litter decomposition contributes only marginally to soil respiration. This result is in agreement with recent studies in temperate forests (Ngao *et al.* 2005), but it contrasts with those obtained in a tropical plantation of eucalypts in Congo where litter mass accounted for most of the spatial variability (Epron *et al.* 2004). In our study, spatial variation in soil carbon content correlated well with that of root density, and since soil carbon content, root density, bulk density and soil respiration are all correlated together, it is almost impossible to clearly identify the cause and effect. However, these results strongly suggest that root

dynamics are an important determinant of soil respiration in this ecosystem.

In conclusion, spatial variation in soil respiration in a tropical rain forest in French Guiana was closely related to topographic position and soil type. Increasing soil water content and bulk density and decreasing root biomass and soil carbon content from hilltops (vertically drained hypoferralic Acrisol) to bottomlands (haplic Gleysol) explained most of the variation in soil respiration among topographic positions. These results will help to stratify further field experiments designed to establish soil or ecosystem carbon balance or to elucidate relationships between soil carbon balance and species diversity. These correlation analyses also help to identify the underlying determinants of spatial variations in soil respiration, thereby contributing to more mechanistic models of soil respiration.

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