Carbon, nitrogen and phosphorus allocation in agro-ecosystems of a West African savanna
II. The soil component under semi-permanent cultivation

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Abstract
The assessment of carbon (C), nitrogen (N) and phosphorus (P) in agro-ecosystems of West African savannas (WAS) may be a useful tool to define sustainable intensification schemes needed to respond to the rapid increase in local populations as well as global change issues. Changes in soil properties, and particularly in the soil organic matter status, under semi-permanent cultivation were thus examined through a groundnut crop-fallow chronosequence in southern Senegal. The effect of fallowing was mainly restricted to the 0–20 cm soil layer and hardly affected soil physical properties. In this layer, steady improvements were recorded for Mg and Ca contents. Carbon and N amounts increased by 30%, and by 50% for available P (P_{obs}) within the very first year of fallow and then remained steady (C and N) or dropped back to levels recorded for crops (P_{obs}). The rapid initial change in organic status after crop abandonment was attributed to fast recovery of woody vegetation. The steady soil organic matter (SOM) content in oldest fallows compared to young fallows probably resulted from poor protection of soil organic matter from oxidation during biological activity. This hypothesis was confirmed by mesh-bag experiments, which indicated that >40–60% of decaying woody root biomass disappeared after 6 months of in situ incubation. In fallow systems in southern Senegal, soil fertility may in fact rely at least as much on fast organic matter cycling in soil food webs as on SOM build-up. Carbon storage in the soil-plant system of mature fallow ecosystems was only 27 t C ha\(^{-1}\) higher than in crops and consisted mainly of pools with fast turnover. Consequently, the potential of semi-permanent cultivation for C sequestration in the WAS will be rather indirect, by a shift to more intensified practices, thus avoiding the conversion of dense forests to cropping in more humid areas. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Carbon; Nitrogen; Phosphorus; Root decomposition; Savanna; Senegal; Semi-permanent cultivation; Soil

1. Introduction
Organic matter (OM) in plants and soil is a versatile tool for sustaining a large proportion of the fertility of farming systems in West African savannas (WAS). Coarse-textured, heavily leached soils are widespread,
and their chemical (pH, cation exchange capacity or CEC) and physical (porosity, stability) properties rely heavily on soil organic matter (SOM) content (Jones and Wild, 1975; Asadu et al., 1997). Moreover, OM inputs are the main source of energy for below-ground biota, thereby driving biological fertility (Brown et al., 1994). This and global change issues related to carbon (C) cycling are the reasons why there is a growing need to assess C, N and P allocation in WAS agro-ecosystems. Published studies on C, N and P dynamics in soil under semi-permanent or shifting cultivation in the WAS are still rare (Tiessen et al., 1998; Harmand et al., 2000), and most concern humid climates (Nye and Greenland, 1960; Woomer et al., 2000).

Quantification of C, N and P in the plant-soil component related to land management was carried out in a mixed-farming system in southern Senegal. A previous study has documented the dynamics of plant biomass and its related nutrients during the crop-fallow cycle (Manlay et al., 2001a). The present paper is concerned with soil C, N and P status during the crop-fallow cycle, while the last part of the study focuses on element budgets in the soil/plant components under continuous cultivation (Manlay et al., 2001b).

From a methodological point of view, agro-ecological interpretation of OM allocation in soil throughout a crop-fallow chronosequence may be significantly improved by (1) taking into account the possible effect of some intrinsic soil properties such as texture on SOM status (Feller and Beare, 1997), and (2) discriminating the functional SOM pools affected by changes in land use. Particle-size soil fractionation allows differentiation between pools carrying out storage, exchange and sorption functions (fine elements) and those fulfilling more biological functions (short term C, N and P mineralisation processes in the coarse fraction) (Feller et al., 2000).

While many studies have been made on the impact of clearing primary vegetation on soil properties, little is known about the impact of clearing on the dynamics of below-ground plant biomass. When fallow is manually converted to cropping, only rooting systems are spared (Floret et al., 1993). In southern Senegal, stumps may play a key role in enhancing the fertility of the plant-soil system, provided they survive cropping (Manlay et al., 2000; Manlay et al., 2001a). However, removing stumps before cropping is becoming a common practice in the WAS due to increasing mechanised tillage. This practice calls into question the sustainability of semi-permanent cultivation, since it can deeply affect soil physical and chemical properties. So far, the fast decay of woody rooting systems that may account for such negative trends has rarely been quantified in semi-permanent cropping systems in dry and sub-humid tropics.

This paper (a) describes some relationships between soil properties, with the focus on organic status and texture during the fallow period, (b) defines temporal thresholds of evolution for soil C, N and available phosphorus, (c) quantifies post-fallow decay of rooting systems and related N and P inputs to the soil.

2. Methods

2.1. Site characteristics

The study was carried out between 1995 and 1997 in the village of Sare Yorobana (12° 49’ N–14° 53’ W), High Casamance, in southern Senegal. A detailed description of climate, vegetation and agricultural practices is given in Manlay et al. (2001a). The following two land use units are considered:

1. a plateau with ferric Lixisols (FAO, 1998) characterised by kaolinite clay type;
2. a glacis, with soils similar to those on the plateau (haplic Lixisols), but with slightly less clay accumulation in the deepest layer. This unit is under continuous cropping and some plots are under semi-permanent cultivation.

2.2. Sampling schemes

Details of the sampling design are described in Manlay et al. (2001a). Briefly, for six groundnut (Arachis hypogaea L.) plots (coded as GN) previously assessed for above- and below-ground biomass, soil samples were taken from small pits dug at each corner of four subplots (4 m × 4 m). In the 11 fallow plots (coded as FA), soil was sampled in a pit at 1-m intervals along a 20-m long transect.

At each site, soil and bulk density (100 cm³ core cylinder) were taken in 10 cm increments to a depth of 40 cm. Deeper sampling would not have changed the interpretations, since most properties are unlikely
to be much influenced by land use below this depth in this kind of soil (Detwiler, 1986).

2.3. Soil analyses

Soil samples were cautiously sieved (at 2 mm) and oven-dried at 105°C for 24 h. Samples were pooled and one analysis was made for each plot and/or soil layer. Soil pH was measured using a 1:2.5 soil/water or KCl solution. Total organic C of non-fractionated (NF) soil was measured after dichromate oxidation, N determined with the Kjeldahl method and soil available P with the Olsen method modified by Dabin (1967) soil total P was not determined, and \( P_{\text{OD}} \) stands for “soil available-P” (phosphorus in plant biomass refers to total P and is denoted \( P_t \)). Exchangeable cations were extracted with \( \text{CH}_3\text{COONH}_4 \) at pH = 7. The CEC was measured by saturating soil with \( \text{CaCl}_2 \cdot 2\text{H}_2\text{O} \) then exchanging Ca with K. Mineral particles of the clay (CLAY), fine (FSILT) and coarse (CSILT) silt, and fine (FSAND) and coarse (CSAND) sand fractions were collected by mechanical analysis after the destruction of organic matter by \( \text{H}_2\text{O}_2 \) and dispersion in \( \text{NH}_4\text{Cl} \). Mass water content was determined at a suction equivalent to pF 2.5 (0.322 atm) and pF 4.2 (14.5 atm). These methods are fully described in Page et al. (1989).

Amounts of C, N and \( P_{\text{OD}} \) in soil were obtained by crossing soil bulk density measurements with C, N and P contents. To assess which SOM functions were affected by fallowing, particle-size fractionation was performed on fractions 0–50 and 50–2000 μm of samples of the 0–10 and 10–20-cm layers, according to the simplified, wet-sieving method from Gavinelli et al. (1995). Total C and N from soil size fractions were determined by wet combustion (Fisons elemental analyser Na2000 Carlo Erba). Results were expressed in g of C per kg of fraction and per kg of soil. Carbon content of both fractions allowed estimation of C partitioning between coarse and fine soil fractions, assuming that losses of water-soluble carbon due to wet particle-size fractionation were negligible and that the bulk density of both fractions was equal.

2.4. In situ root decomposition

Post-fallow root dynamics after stump removal was assessed with a mesh-bag decomposition experiment. Roots of Combretum glutinosum Perr., the most widespread tree species in fallows in the region, were sampled at the end of the dry season, washed, oven-dried at 70°C to a constant weight and sorted into three diameter classes (0–2, 2–5 and 5–10 mm). These were put in stainless-steel 3 mm mesh bags filled with local soil and buried 15 cm deep in a 15-year old fallow plot at the onset of the rainy season. Vegetation was cleared and soil left bare during the course of the whole experiment. A total of 20 bags of each diameter class were removed every 6 months over a period of 2 years. Remaining roots were washed under water and oven-dried before weighing. Initial and final ash contents were measured after calcination for 3 h at 500°C. The decomposition rates determined from this experiment were used to estimate the rate of tree root disappearance after the clearing of a young and an old fallow, assuming that (1) stumps were killed or removed, (2) the decomposition rate remained constant irrespective of soil depth down to 40 cm and tree species (which was confirmed in a running experiment with roots of the three other main woody species of the ecozone, unpublished data). Initial root biomass was set as the mean value found for young fallows (aged 1–9 years) and old fallows (aged 10 years and more) at the study site (Manlay et al., 2001a).

2.5. Data analyses

Principal component analyses (PCA) were computed with ADE 4 software (Thioulouse et al., 1997). Other statistical analyses were done using CORR, GLM, NLIN and REG procedures from SAS software 6.14 (Hatcher and Stepanski, 1994).

2.5.1. Multivariate analyses

Rapid appraisal of relations between soil properties and the changes that occurred during the crop-fallow succession was made for each soil layer by performing multivariate analyses and computing Spearman’s correlation coefficients (proc CORR) for the following soil variables: C (total, and in fine and coarse fractions for layers 0–10 and 10–20-cm only), N, C:N ratio, \( P_{\text{OD}} \), pH in H2O and KCl, Ca, Mg, Na, K, CEC, saturation rate (S), five-fraction granulometry, bulk density, clay + fine silt, pF 2.5 and pF 4.2. Principal component analyses were computed on the correlation matrix.
2.5.2. Univariate analyses

The synchronic method requires that properties inherent to soil, likely to influence the values of tested parameters, be the same in all plots of the chronosequence. This condition is seldom fulfilled in field experimentation. However, such a variable may be introduced as a covariate in the linear model used for the analysis of variance (Anova), assuming that its range of variation is not too wide, so that bio-physical processes differ only in intensity. Particular attention should be paid to texture as a possible bias for statistical interpretations trying to link SOM status to land management (Jones and Wild, 1975). Following the findings of Feller (1993), the clay + fine silt content was introduced as a covariate in Anovas.

Results from Manlay et al. (2001a) demonstrated that a threshold for the biomass of most plant components was reached after 10 years of fallowing at the study site. Plot replicates were thus clustered in three groups: groundnut crops (GN), young fallows (YF) aged <10 years, and old fallows (OF). Proc GLM was used on ranks of data due to the small number of repeated measures and uncertainty about normality of distributions of data and residues, as recommended by Potvin and Roff (1993). Pair-wise t-tests were performed on least-square means in order to segregate treatments with different effects on the level of the variable tested (α = 0.05).

2.5.3. Modelling of C storage in soil

The following exponential accumulation model derived from Nye and Greenland (1960) was fitted to carbon storage data:

\[ S(t) = S_0 - (S_e - S_0) \exp\left(-\frac{A}{S_e} t\right) \]  

where \( S_0 \) and \( S_e \) are the C stocks, respectively, at \( t = 0 \) and \( t \to +\infty \) (equilibrium), and \( A \) is the annual C input to the soil.

The NLIN and REG procedures were used for the estimation of non-linear regression parameters. Model adequacy was estimated testing \( R^2 \), slope and intercept of the regression of modelled versus observed data (Pavé, 1994). Annual C input “A” was not allowed to exceed 20 t ha\(^{-1}\) per year, in agreement with upper net plant productivity figures reported for subhumid tropical ecosystems (Menaut and César, 1979).

3. Results

3.1. Interrelations between soil properties throughout the crop-fallow succession

Correlation analysis indicated the following statistically significant links between variables for each of the following soil layers (\( P(\text{H}_0: R_s = 0) < 0.05 \)).

3.1.1. The 0–10 cm soil layer

Carbon (total, and in fine and coarse fractions) and N were highly positively correlated (data not shown). Other chemical variables such as pH (KCl), Ca, Mg, CEC and S were also positively related to total C and N. Clay + fine silt was positively correlated with total C and N. The pF 4.2 and clay, and pH (KCl and H\(_2\)O) and S, were positively correlated with each other (as well as for deeper layers). In the 0–10 cm layer, the first principal component (PC) (relative inertia: 35%) may be interpreted as “SOM-related nutrient status”, since its highest loadings were provided by C (total and in fractions), N, CEC, Ca, Mg and S (Fig. 1a1).

Old fallows (associated with high SOM status) were clearly separated from groundnut crops along this PC (Fig. 1a2). Available P (and coarse texture to a lesser extent) was the main contributor to PC2. Young fallows were more clearly associated with high P\(_{OD}\) and...
Fig. 1.
Table 1
Effect of land management (fallowing) and texture (clay + fine silt content) on soil physical properties.

<table>
<thead>
<tr>
<th>Layer (cm)</th>
<th>Groundnut field; mean (±S.E.) (n = 6)</th>
<th>Young fallow; mean (±S.E.) (n = 6)</th>
<th>Old fallow; mean (±S.E.) (n = 5)</th>
<th>F Management Texture Management x Texture</th>
<th>Overall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clay + fine silt content (%)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0–10</td>
<td>11.3 ± 1.2</td>
<td>12.4 ± 0.8</td>
<td>14.1 ± 0.5</td>
<td>3.2</td>
<td></td>
</tr>
<tr>
<td>10–20</td>
<td>17.1 ± 1.3</td>
<td>16.5 ± 1.1</td>
<td>17.6 ± 1.1</td>
<td>0.1</td>
<td></td>
</tr>
<tr>
<td>pH 2.5 (g H₂O 100 g⁻¹ soil)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0–10</td>
<td>6.95 ± 0.08 a</td>
<td>4.95 ± 0.48 b</td>
<td>8.28 ± 1.74 ab</td>
<td>3.1</td>
<td>0.1</td>
</tr>
<tr>
<td>10–20</td>
<td>8.02 ± 1.13 a</td>
<td>5.53 ± 0.19 b</td>
<td>8.52 ± 1.75 a</td>
<td>0.1</td>
<td>1.5</td>
</tr>
<tr>
<td>pH 4.2 (g H₂O 100 g⁻¹ soil)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0–10</td>
<td>7.08 ± 0.34</td>
<td>3.06 ± 0.33</td>
<td>3.74 ± 0.33</td>
<td>1.0</td>
<td>0.6</td>
</tr>
<tr>
<td>10–20</td>
<td>4.03 ± 0.46</td>
<td>4.00 ± 0.12</td>
<td>4.28 ± 0.21</td>
<td>3.1</td>
<td>1.9</td>
</tr>
<tr>
<td>Bulk density (kg dm⁻³)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0–10</td>
<td>1.52 ± 0.01 b</td>
<td>1.52 ± 0.02 a</td>
<td>1.50 ± 0.02 a</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>10–20</td>
<td>1.47 ± 0.03 b</td>
<td>1.54 ± 0.01 a</td>
<td>1.52 ± 0.01 ab</td>
<td>1.8</td>
<td>0.3</td>
</tr>
</tbody>
</table>

*Two mean values with different letters differ significantly in their LS means (α = 0.05; pair-wise t-test).

3.1.2. The 10–20 cm soil layer
The C and N were only correlated with CEC and density. The clay + fine silt was correlated with pH (−), CEC (+), and S (−). The PCA provided limited information in this layer (Fig. 1b1). Only 26% of the total variance was explained by PC1, which was described by pH, fine texture and Ca, and was thus difficult to interpret.

3.1.3. The 20–30 and 30–40 cm soil layers
All chemical variables, except cation contents, were well correlated with fine texture, especially in the 30–40 cm layer. In these layers, the first PC extracted accounted for 36% of total variance of the data set, and could be termed as “clay and clay-related organic status” (Fig. 1c,d). The second PC was best described by cation contents. Like for the 10–20 cm soil layer (Fig. 1b2) Gn, YF and OF plot clusters could not be clearly ordinated according to both PCs, while preeminent textural variations below 20 cm were confirmed by Anovas, which showed significant interactions between land management and texture, and made interpretation of the effect of both factors on soil properties difficult (data not shown).

Overall, PCA and Anovas indicated that (1) in the 0–10 cm layer fallowing had a noticeable and positive effect on organic and organic-related nutrient status, except for POD (2) in the 10–20 cm layer fallowing became less clear, mainly concerning C, N and Mg, (3) in the 20–40 cm layer, chemical (except cations) properties were influenced by texture rather than by management.

3.2. SOM quality
Soil organic matter quality was investigated using several different criteria: the C:N ratio of organic matter of the non-fractionated soil, and the C concentration and content, and C:N ratio of 0–50 and 50–2000 µm size fractions.
Table 2

<table>
<thead>
<tr>
<th>Layer (cm)</th>
<th>Groundnut field; mean (±S.E.) (n = 6)</th>
<th>Young fallow; mean (±S.E.) (n = 6)</th>
<th>Old fallow; mean (±S.E.) (n = 5)</th>
<th>F Management Texture Management × Texture Overall</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH (KCl)</td>
<td></td>
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</tr>
<tr>
<td>0–10</td>
<td>5.15 ± 0.12</td>
<td>5.24 ± 0.09</td>
<td>5.33 ± 0.11</td>
<td>0.2 1.1 0.2 0.9</td>
</tr>
<tr>
<td>10–20</td>
<td>4.63 ± 0.17</td>
<td>4.95 ± 0.14</td>
<td>4.88 ± 0.18</td>
<td>0.2 9.2* 0.0 2.8*</td>
</tr>
<tr>
<td>Ca (mg 100 g⁻¹ soil)</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>0–10</td>
<td>1.52 ± 0.13</td>
<td>1.60 ± 0.19</td>
<td>1.94 ± 0.39</td>
<td>0.5 0.0 0.5 0.6</td>
</tr>
<tr>
<td>10–20</td>
<td>1.06 ± 0.17</td>
<td>1.20 ± 0.2</td>
<td>1.42 ± 0.43</td>
<td>0.0 2.6 0.0 0.8</td>
</tr>
<tr>
<td>Mg (mg 100 g⁻¹ soil)</td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>0–10</td>
<td>0.36 ± 0.03 c</td>
<td>0.48 ± 0.03 b</td>
<td>0.64 ± 0.01 a</td>
<td>2.7 1.0 0.5 12.9***</td>
</tr>
<tr>
<td>10–20</td>
<td>0.32 ± 0.01 b</td>
<td>0.45 ± 0.05 ab</td>
<td>0.60 ± 0.05 a</td>
<td>4.8* 4.7 1.7 7.4*</td>
</tr>
<tr>
<td>Na (mg 100 g⁻¹ soil)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0–10</td>
<td>0.01 ± 0.005</td>
<td>0.02 ± 0.006</td>
<td>0.01 ± 0.005</td>
<td>1.1 0.0 1.5 0.9</td>
</tr>
<tr>
<td>10–20</td>
<td>0.00 ± 0.002</td>
<td>0.01 ± 0.003</td>
<td>0.01 ± 0.008</td>
<td>3.7 0.0 5.9* 4.3*</td>
</tr>
<tr>
<td>K (mg 100 g⁻¹ soil)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0–10</td>
<td>0.04 ± 0.004</td>
<td>0.06 ± 0.008</td>
<td>0.04 ± 0.008</td>
<td>1.5 0.4 0.8 1.5</td>
</tr>
<tr>
<td>10–20</td>
<td>0.04 ± 0.004</td>
<td>0.06 ± 0.008</td>
<td>0.04 ± 0.009</td>
<td>4.9* 0.6 3.0 2.2</td>
</tr>
<tr>
<td>CEC (mg 100 g⁻¹ soil)</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>0–10</td>
<td>2.31 ± 0.1</td>
<td>2.54 ± 0.1</td>
<td>2.65 ± 0.08</td>
<td>1.3 3.3 1.9 4.8*</td>
</tr>
<tr>
<td>10–20</td>
<td>2.49 ± 0.08</td>
<td>2.44 ± 0.07</td>
<td>2.15 ± 0.14</td>
<td>1.4 7.1* 0.3 2.4</td>
</tr>
<tr>
<td>Saturation rate (%)</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>0–10</td>
<td>74.5 ± 5.2</td>
<td>84.8 ± 7.4</td>
<td>98.4 ± 11.9</td>
<td>0.4 0.3 0.2 0.6</td>
</tr>
<tr>
<td>10–20</td>
<td>57.3 ± 7.4</td>
<td>74.0 ± 7.4</td>
<td>96.0 ± 20.5</td>
<td>0.4 4.9* 0.0 2.2</td>
</tr>
</tbody>
</table>

* Two mean values with different letters differ significantly in their LS means (α = 0.05; pair-wise t-test).

b Management × texture: interaction between management and texture.

P (H₀ : F₀ < Fₐ ) < 0.05.

P (H₀ : F₀ < Fₐ ) < 0.01.

P (H₀ : F₀ < Fₐ ) < 0.001.

The C:N ratio of the NF soil did not vary significantly during the fallow period, averaging 11.6 ± 0.3 (data not shown). Carbon recovery rate was 95 ± 2% (n = 31). Carbon content (g kg⁻¹ of fraction) in the 0–50 μm fraction was 10–20 times as high as than in the coarse one. However, fallow mainly affected the 50–2000 μm fraction, whose C content (g kg⁻¹ of soil) doubled after crop abandonment (Table 3). In the 0–10 cm layer the contribution (g C kg⁻¹ of soil) of the C associated to the fraction 0–50 μm increased steadily by 40% from GN to OF. A similar increase was recorded for the coarse fraction, the difference being significant within the first years of fallow succession. Observations for the 10–20 cm layer were similar, except C content of the fine fraction that remained stable in each stage of the succession. The C:N ratio of fine and coarse fractions rose steadily and significantly throughout the succession at both depths; but progression was stronger in the coarse fraction than in the fine one.

Thus, fallowing significantly affected the distribution of carbon between the particle-size fractions in the 0–10 (and, to a lesser extent, 10–20 cm) layer. Although it accounted for only 20% of total soil organic carbon amount, the coarse size fraction was responsible for half of the total increase.

3.3. Patterns of soil C, N and P storage

Carbon and N storage (respectively 12.2/22.3 and 1.001/1.92 t ha⁻¹ in the 0–20/40 cm layers of groundnut fields) increased by 30% in the 0–20 cm layer (20%
Table 3
Effect of land management (fallowing) and texture (clay + fine silt content) on soil organic matter quality as assessed by C concentration and content, and C:N ratio in fine and coarse soil fractionsa

<table>
<thead>
<tr>
<th>Layer (cm)</th>
<th>Fraction (μm)</th>
<th>Groundnut field: mean (± S.E.) (n = 6)</th>
<th>Young fallow: mean (± S.E.) (n = 5)</th>
<th>Old fallow: mean (± S.E.) (n = 5)</th>
<th>F Management Texture Management X Texture Overall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carbon content (g kg⁻¹)</td>
<td>0–10</td>
<td>0–50</td>
<td>15.21 ± 0.77 b</td>
<td>18.32 ± 0.64 a</td>
<td>18.99 ± 1.37 a</td>
</tr>
<tr>
<td></td>
<td>50–200</td>
<td>1.11 ± 0.1 b</td>
<td>1.94 ± 0.1 a</td>
<td>1.92 ± 0.11 a</td>
<td>7.3**</td>
</tr>
<tr>
<td></td>
<td>10–20</td>
<td>0–50</td>
<td>10.13 ± 0.41</td>
<td>11.23 ± 0.54</td>
<td>10.80 ± 0.64</td>
</tr>
<tr>
<td></td>
<td>50–200</td>
<td>1.46 ± 0.19</td>
<td>1.41 ± 0.33</td>
<td>1.22 ± 0.32</td>
<td>0.7</td>
</tr>
<tr>
<td>Carbon content (g kg⁻¹ soil)</td>
<td>0–10</td>
<td>0–50</td>
<td>3.14 ± 0.15 c</td>
<td>4.04 ± 0.21 b</td>
<td>4.43 ± 0.18 a</td>
</tr>
<tr>
<td></td>
<td>50–200</td>
<td>0.87 ± 0.07 b</td>
<td>1.55 ± 0.09 a</td>
<td>1.47 ± 0.11 a</td>
<td>8.7**</td>
</tr>
<tr>
<td></td>
<td>10–20</td>
<td>0–50</td>
<td>2.70 ± 0.1</td>
<td>2.78 ± 0.14</td>
<td>2.77 ± 0.08</td>
</tr>
<tr>
<td></td>
<td>50–200</td>
<td>0.48 ± 0.14</td>
<td>1.05 ± 0.25</td>
<td>0.90 ± 0.24</td>
<td>0.8</td>
</tr>
<tr>
<td>C:N in fractions</td>
<td>0–10</td>
<td>0–50</td>
<td>12.7 ± 0.3 e</td>
<td>13.4 ± 0.3 ab</td>
<td>14.6 ± 0.5 a</td>
</tr>
<tr>
<td></td>
<td>50–200</td>
<td>29.4 ± 2.3 b</td>
<td>37.3 ± 1.1 a</td>
<td>48.7 ± 2.7 a</td>
<td>8.2**</td>
</tr>
<tr>
<td></td>
<td>10–20</td>
<td>0–50</td>
<td>11.9 ± 0.3</td>
<td>12.8 ± 0.1 ab</td>
<td>13.7 ± 0.5 a</td>
</tr>
<tr>
<td></td>
<td>50–200</td>
<td>33.2 ± 4.6 b</td>
<td>51.1 ± 6.7 a</td>
<td>82.3 ± 14.4 a</td>
<td>4.9*</td>
</tr>
</tbody>
</table>

a Two mean values with different letters differ significantly in their LS means (α = 0.05; pair-wise t-test).

Table 4
Estimates for parameters of a regression of S = amount of C on t = length of fallow according to an exponential accumulation modelb

<table>
<thead>
<tr>
<th>Fraction (μm)</th>
<th>Layer (cm)</th>
<th>S₀ (g C m⁻²)</th>
<th>S₀ (g C m⁻²)</th>
<th>A (g C m⁻² per year)</th>
<th>B₀</th>
<th>F</th>
<th>P &gt; F</th>
<th>P (B₀ = 0)</th>
<th>P (B₀ = 1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–2000</td>
<td>0–10</td>
<td>6.84</td>
<td>9.06</td>
<td>20.00</td>
<td>0.36</td>
<td>8.5</td>
<td>*</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>10–20</td>
<td>5.39</td>
<td>6.17</td>
<td>20.00</td>
<td>0.23</td>
<td>4.6</td>
<td>*</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>0–20</td>
<td>12.37</td>
<td>15.52</td>
<td>20.00</td>
<td>0.41</td>
<td>10.5</td>
<td>**</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>0–50</td>
<td>0–10</td>
<td>5.37</td>
<td>6.78</td>
<td>6.52</td>
<td>0.26</td>
<td>5.2</td>
<td>*</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>10–20</td>
<td>4.90</td>
<td>3.01</td>
<td>0.04</td>
<td>0.05</td>
<td>0.8</td>
<td>***</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>0–20</td>
<td>9.99</td>
<td>11.50</td>
<td>20.00</td>
<td>0.14</td>
<td>2.5</td>
<td>***</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>50–2000</td>
<td>0–10</td>
<td>1.47</td>
<td>2.39</td>
<td>20.00</td>
<td>0.53</td>
<td>17.0</td>
<td>***</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td>10–20</td>
<td>0.77</td>
<td>1.38</td>
<td>2.96</td>
<td>0.25</td>
<td>5.0</td>
<td>*</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>0–20</td>
<td>2.24</td>
<td>3.93</td>
<td>20.00</td>
<td>0.56</td>
<td>18.9</td>
<td>***</td>
<td>**</td>
<td>**</td>
</tr>
</tbody>
</table>

b Two mean values with different letters differ significantly in their LS means (α = 0.05; pair-wise t-test).

A mathematical expression of the model is: $S(t) = S_0 - (S_1 - S_0) \exp(-\frac{t}{\lambda})$ where $S_0$ and $S_1$ are the C stocks at $t = 0$ and when $t \rightarrow +\infty$ (equilibrium), respectively, and $A$ is the annual C input to the soil.

* $P (B₀, F_{B₀} = F_{B₀} = 0) < 0.05$

** $P (B₀, F_{B₀} = F_{B₀} = 0) < 0.01$

*** $P (B₀, F_{B₀} = F_{B₀} = 0) < 0.00$
increases in available P were recorded within the very first year of fallow, amounts then rapidly dropped back to those of the crops (Fig. 3).

When the whole ecosystem was considered (Fig. 4), soil (0–40 cm) contribution to C and N storage dropped rapidly after crop abandonment. The increase in the proportion contributed by the plant component was particularly high for P (only available P in soil considered).

3.4. Post-fallow dynamics of root biomass

Dead tree root biomass disappeared rapidly (Fig. 5). After the first 6 months of in situ incubation, highest initial decomposition rates were recorded for the finest roots: 61% versus 50% and 41% of mass loss for the 2–5 and 5–10 mm diameter classes, respectively. As incubation continued, these rates decreased and remained constant beyond the second year.

These results were applied to simulate the decay of root biomass after the clearing of two hypothetical young and old fallows in which stumps would have been removed (Fig. 6). Estimated disappearance (that is, oxidation or simple spatial reallocation in the plant-soil system) of dry matter (DM), C, N and P$_r$ related to decaying root biomass would be massive within the first 6 months following the clearing of the fallow, amounting to 4.0/9.3 t DM, 1.4/3.3 t C, 20/43 kg N and 1.1/3.4 kg P$_r$ ha$^{-1}$, depending on the age of fallow (young/old). Rates of disappearance...
would drop by nearly two-thirds during the second cropping season.

4. Discussion

4.1. Influence of intrinsic soil properties

Low-activity of kaolinite suggests that the strong control exerted by fine elements over soil chemical properties (e.g. CEC) below a depth of 20 cm was certainly indirectly mediated by organic matter (Fig. 1c,d) (Asadu et al., 1997). This control led to serious problems in accurately assessing the impact of fallowing on soil properties in the 20–40 cm layer, although it is probably weak at this depth. Clay properties and the low values measured for Na and K, which imply serious analytic error, may also explain the weak correlation between cationic status and fine element content. Low clay content, which prevents a strong soil structure build-up, and regular hoeing and sometimes ploughing, which results in increased porosity, might both account for the absence of effects of management and texture on bulk density (Table 1). The poor correlation between pH 2.5 (but not pH 4.2) and clay content indicates that some factors controlling water status may still have to be identified for these soils (Fig. 1).

4.2. Nutrient balance of the crop-fallow system

The increase in N and P (plant P + soil P) for the whole system after one year of fallow was striking (Fig. 4). But the efficiency of some young tropical fallows or pastures in achieving fast recovery of substantial amounts of soil N and available P is well established (Friesen et al., 1997; Brand and Pfund, 1998). Faced with high soil chemical constraint, savannas have developed specific nutrient-conservative strategies (Myers et al., 1994), and C inputs to the soil do not account fully for N accumulation recorded during the early stages of fallowing. Three mechanisms might explain the results obtained in Sare Yorobana fallows: (1) nutrient saving thanks to short recycling from root litter to rooting system and nitrification inhibition (Abbadie et al., 1992; Lata et al., 1999), (2)
nutrient pumping from deep soil layers, accounting for the regular increase in Mg and Ca, and maybe P to a certain extent during the first year; however, this phenomenon may be seriously restricted in Lixisols due to shallow root extension (Breman and Kessler, 1995; Manlay et al., 2001a), (3) nutrient immobilisation in biomass thanks to high plant efficiency in extracting assimilable elements such as phosphorus (Friesen et al., 1997; Sirois et al., 1998).

Soil P; P\textsubscript{OD} ratio is quite stable (28.3 \pm 2.9; n = 4) in Sare Yorobana fallows (Manlay, unpub. data), thus making P\textsubscript{OD} fluctuations a reliable indicator of variations in total P. The shape of P storage in soil as a function of fallow length may in fact result from

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**Fig. 4.** Carbon, N and P (soil: available P only) storage in the plant-soil system at three main stages of the crop-fallow succession. Young fallow: aged 0–9 years. Old fallow: aged 10 years and more. Figures for stocks in plant biomass derived from Manlay et al., 2001a.
Fig. 5. Root decomposition dynamics of Combretum glutinosum Perr. after clearing of a 15 year-old fallow measured during a mesh-bag experiment. Vertical bars stand for standard error (n = 20).

A balance between mechanisms 2 (P input) and 3 (P immobilisation in plants) (Fig. 3). In the long term, P availability together with water supply, must account for the fast blocking of tree standing biomass in Sare Yorobana fallows >10 years old (Akpo, 1998; Sirois et al., 1998; Manlay et al., 2001a).

4.3. Soil organic status after crop abandonment

Soil carbon dynamics occurring during fallow is a vital issue for later cropping: mineral fertilisation without organic amendments results in SOM mineralisation and subsequent soil structure disruption, a decrease in pH and an increase in aluminic toxicity, and thus barely sustains productivity in West Africa (Pieri, 1989). The present study confirms the well-documented, prominent control of SOM over many other chemical properties in the upper layer (Fig. 1a).

The dramatic decline in soil carbon content recorded during cropping after clearing tropical primary forests or woodlands is now well established and understood (Maass, 1995). However, the potential of fallowing to reverse SOM losses due to prolonged cultivation remains much more controversial (Szott et al., 1999). Many authors relate significant increases in soil carbon content following crop abandonment (Nye and Greenland, 1960; Areola et al., 1982; Tiessen et al., 1992; Feller, 1993). But their works do not show a consensus about the shape of

Fig. 6. Estimated remaining amounts of dry matter, carbon, nitrogen and phosphorus from the decaying root component after clearing of a young (YF) and old (OF) fallow (stumps removed).
the curve of carbon accumulation as a function of the length of fallow, nor the minimum period of fallow required for a significant improvement in SOM content. At least as many studies carried out under various tropical climates report no significant change in carbon storage after crop abandonment (Breman and Kessler, 1995; Juo et al., 1995; Kotto-Same et al., 1997; Sirois et al., 1998; Scott et al., 1999; Denich et al., 2000 among others). Accurate comparisons between these studies are seriously hindered by the lack of attention paid to interactions between the effect of management and texture (in synchronic approaches). And any judgement about the capacity of fallowing to restore the organic content of a soil can only be made in the light of how far the SOM content is from equilibrium level under native vegetation (Nye and Greenland, 1960; Scott et al., 1999), which is often poorly documented. Finally, the carbon storage capacity of fallowing may also depend on the tree species that comprise the secondary vegetation (Harmand et al., 2000).

In Sare Yorobana the model of C accumulation during the fallow period agrees (to some extent) with the exponential model of Nye and Greenland (1960), but to a particular form of it: the strong initial increase is quickly followed by an equilibrium stage that is reached within the second year of fallowing (Fig. 2). This trend contrasts with those in previously cited studies. On the other hand, more than a half of C accumulation recorded for the 0–20 cm layer occurs in the 50–200 μm size fraction; SOM of that fraction has a fast turnover and fulfils biological functions such as C and nutrient supply to roots, soil microflora and fauna (Feller et al., 2000). Thus, a large part of SOM status improvement is not likely to have much impact on soil nutrient status and will vanish shortly after crop conversion—although in Sare Yorobana, fallowing has been shown to cause C input fluxes up to at least 3.6 t ha⁻¹ per year in old stands (Manlay et al., 2001a).

Several factors may explain the weak and fragile response of local soils to fallow management. In the plateau soils of High Casamance, the sand-loamy texture does not allow for efficient SOM protection against microbial oxidation, leaching and erosion losses (Feller and Beare, 1997). Seasonal rainfall, and soil moisture and temperature patterns unfavourable to humification are the other abiotic reasons for limited SOM storage. Harvest of deadwood by people, as well as CO₂ mineralisation induced by fire may be other reasons, although the effect of fire on the SOM content of young fallows has recently been questioned (Masse et al., 1997).

4.4. Fallowing as a tool for the recovery of biological control over ecosystem fertility

Massive root decay following fallow clearing testifies to intense biological activity (even during the dry season), suggesting that the growing control exerted by biological activity over SOM dynamics is a crucial factor limiting the carbon storage capacity of soils of local mature secondary ecosystems. This is supported by other works that report an increase in biomass and in the diversity of soil macrofauna following crop abandonment in Sare Yorobana and central Senegal (Sarr et al., 1998; Fall et al., 2000; Derouard, unpublished data). Termites may control more than 90% of net carbon production of the ecosystem (Jones, 1990). They and earthworms improve SOM physical and chemical availability to micro-organisms (Lavelle et al., 1998), contributing to higher SOM turnover under tropical conditions.

Massive “grazing” of organic inputs by heterotrophic biota is certainly of vital agro-ecological importance for the fertility of local agro-ecosystems: both subsequent increases in biomass and diversity recorded for macrofauna, nematodes (Manlay et al., 2000; Pate et al., 2000) and even mycorrhizal soil infectivity (R. Duponnois, pers. comm.) can increase plant productivity (Villenave and Cadet, 1997).

Furthermore, together with the rooting systems, growing, diversifying biota enhances the resilience and stability of the ecosystem in the face of climatic hazards, poor soil nutrient status and physical stability (Menaut et al., 1985; Brown et al., 1994; Ewel, 1999).

4.5. West African fallow management from the perspective of global change

This study provides information on carbon sequestration potential in savannas as an attempt to mitigate anthropogenic greenhouse emissions, of which 29% would stem from changes in land use in the tropics (Fearnside, 2000).

Carbon dynamics exhibit various trends, depending on the plant or soil component considered (Fig. 4).
What has already been observed under more humid contexts (Woomer et al., 2000) was confirmed in the present study: more carbon is added to the plant than to the soil component after crop abandonment.

According to current slash-and-burn practices, clearing a mature fallow in southern Senegal would release 27 t C ha\(^{-1}\) through immediate burning, later combustion of wood for energy requirements, on-site decomposition of roots, stumps and remaining unburnt twigs and leaves, and mineralisation of a small part of SOM. Nearly half of this value (12.3 t C ha\(^{-1}\)) can be recovered during the first year of fallow. Subsequently the annual rate of storage is only 2 t C ha\(^{-1}\) during the 10 following years of fallow (Manlay et al., 2001a). But long fallows, or at least the protection of rooting systems and stumps during cropping are required. The potential of falling for carbon sequestration in savannas of southern Senegal is thus weak compared to that reported for tropical subhumid and wet forest (8–10 t C ha\(^{-1}\) per year) (Denich et al., 2000; Woomer et al., 2000). What is more, stable carbon gain in the soil fine-size fraction is only 1.5 t Ch a\(^{-1}\) (0-20 cm layer). Thus, sequestration is more likely to happen in pools with high turnover rates (soil coarse fraction, plant biomass), unless wood felling is for construction only. However that may be, the local need for land and the lack of immediate financial return for the farmer from carbon sequestration may well represent the main obstacle in converting African savanna fallows into a carbon sink (Izac and Swift, 1994; Tiessen et al., 1998).

5. Conclusion

Fallowing is an efficient tool for improving some of the chemical properties of Senegalese subhumid savannas. Nevertheless, trends in carbon and nutrient accretion vary greatly among the elements considered. For instance, the increase is initially very high and subsequently nil for carbon or nitrogen, but continuous for Mg and Ca. Fallow efficiency relies on soil texture and crop history, and the results reported in this study apply only to coarse-textured soils subjected to little disturbance. If the limited potential to store carbon in Sare Yoroohana soils has been established, why promote agro-ecological practices aimed at ensuring minimum carbon inputs to the soil?

From the point of view of global change, the answer is simple: a mitigation of anthropogenic carbon release in the atmosphere must be achieved, at acceptable human cost, anywhere, in any component and by any possible means. However, as is true for tropical secondary forests, the contribution of savanna fallows in southern Senegal to the control of greenhouse gas emissions should preferably be indirect (Brown and Lugo, 1990), i.e. by providing local populations with more income from intensified agro-ecosystems, thus limiting the need for land on the northern fringe of humid forests with high carbon storage capacity.

From the point of view of the farmer faced with problems of fertility, (a) in the High-Casamance agro-ecological context of low anthropisation and access to chemical inputs, biological maintenance (in the sense of Izac and Swift, 1994) can play a key role in enhancing soil fertility after crop abandonment, thanks to efficient nutrient conservation strategies, structural integrity supplied by live plant biomass, and functional stability through the enhancement of soil biodiversity (Odum, 1969; Giller et al., 1997), (b) the limited potential of long fallows to increase SOM content compared to young fallows is the energetic cost to pay for such biological maintenance.

Technical solutions for improving falling practices that satisfy both points of view could be direct soil management (e.g. adoption of cover crops and no-tillage). However, the most efficient and feasible improvements in the current socio-economic context are probably vegetation management such as stump-saving and slash-and-mulch clearing, control of fire, and improvement of fallow through dispersed tree plantation.

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References


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