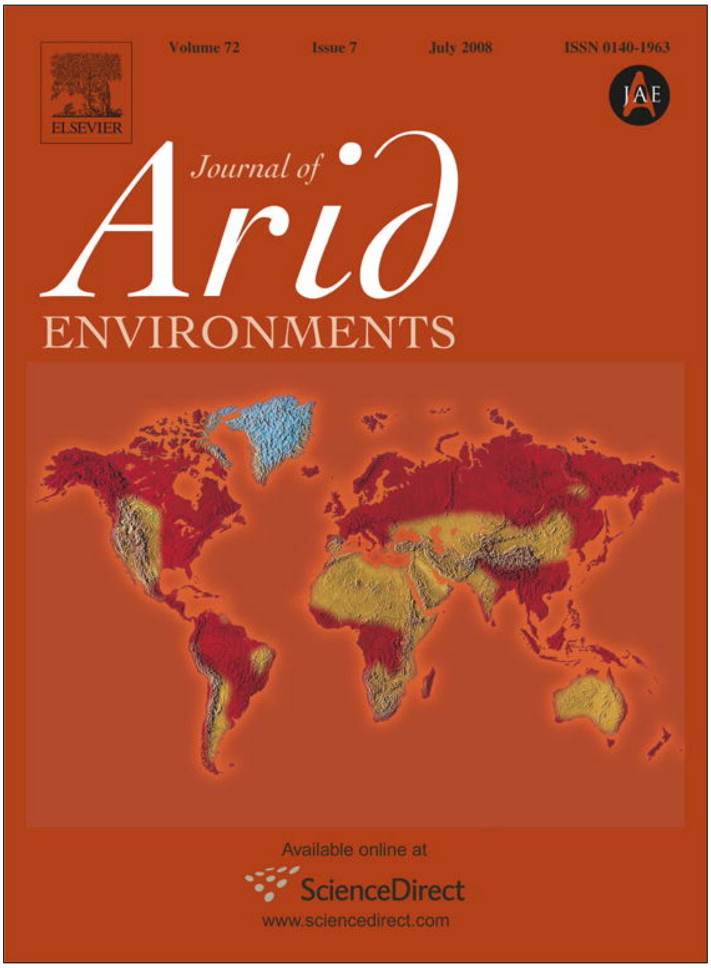
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# Soil fertility and arbuscular mycorrhizal fungi related to trees growing on smallholder farms in Senegal

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**Abstract**

Tree cultivation in the dryland agroecosystems is increasingly advocated as a strategy to protect and reverse soil fertility decline, thus sustaining agricultural production. Woody legumes trees like the Ana tree *Faidherbia albida* (Del.) Chev. host $N_2$-fixing bacteria as well as arbuscular mycorrhizal fungi (AMF), which may contribute to the soil organic carbon pool and soil fertility. The objective of this work was to determine how trees influenced AMF and soil fertility in the agroecosystems of two rural communities (Palmarin and Fimela) of the Saloum Agricultural Eco-Region of Senegal. Smallholder farmers typically cultivated 3–4 fields ranging in size from 0.5 to 2.0 ha with the major crop being millet (*Pennisetum glaucum* L.). Soil fertility was low to medium, with about 1% soil organic matter (SOM), $17 \pm 2.2$ mg Bray-1 P $kg^{-1}$ and $65 \pm 5.8$ mg extractable K $kg^{-1}$ in the fields studied. There were seven times more trees per hectare and greater tree diversity in fields around Palmarin, where the smallholder farmers resided, than in the fields they cultivated in Fimela. Social norms appeared to protect trees inside the residential village, while trees farther away are prone to being cut. The relationships between trees, AMF and soil fertility were examined using exploratory path analysis, a structural equation modeling technique. The path analysis model revealed a direct and significant ($P < 0.05$) impact of trees on SOM and pH, which in turn affected the plant-available nitrogen and phosphorus concentrations. The hypothesized relationships between trees, AMF and soil fertility were not supported.


*Keywords:* Agroforestry; Dryland farming systems; Glomalin; Soil organic matter; West Africa

## 1. Introduction

Many soils in West Africa are highly weathered and have low to moderate fertility (Bationo et al., 1998; Schlecht et al., 2006). Those with sandy to sandy loam surface horizons have low organic matter contents, a low native phosphorus (P) concentration and little cation exchange capacity (Manu et al., 1991). Soil fertility could be improved, but organic inputs are scarce and mineral fertilizers are often out of reach for the

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subsistence farmers of West Africa (Breman and Kessler, 1997). The Serer of Senegal have long used an agroforestry system to maintain agricultural production on a small land base (Pélissier, 1966). This system relies on the Ana tree, *Faidherbia albida* (syn. *Acacia albida* Del.), a leguminous $N_2$-fixing species that provides shade and fodder for animals, organic residues and N for crop production, and edible seeds (Booth and Wickens, 1988). Traditionally, the allocation of fallow and pastoral land for grazing animals, tree cultivation and the use of cereal–legume rotations was directed by the village council (Piéri, 1992). Despite the fragile soils, difficult climatic conditions and restricted land base in Serer country, their agroforestry system supported 75–85 individuals $km^{-2}$ in the 1960s (Pélissier, 1966) and 130 individuals $km^{-2}$ in the 1980s (Garin et al., 1990).

Since 1900, Senegal's population has increased 10-fold and is expected to reach 16 million by 2020. Currently in the West Central Agricultural Region, or "Peanut Basin", population density varies from 150 to 225 inhabitants $km^{-2}$ (Centre de Suivi Écologique, 2000). Such dramatic population growth places unprecedented pressure on land use and natural resources. Between 1965 and 1985, about 23% of the trees around a Serer village in the "Peanut Basin" disappeared due to agricultural expansion, forest harvesting for firewood and charcoal, drought and government policies that encouraged peanut production (Lericollais, 1987). Ganry et al. (2001) reported a decline in the land area set aside for fallow and pastures, less manuring of cropland and the disappearance of non-agricultural crop plants, especially *F. albida*, in Serer country during the same period. Since the early 1990s, the amount of land under fallow has increased slightly in some areas, which is thought to be a consequence of poverty and out-migration from farms, due to the cessation of state subsidies for agricultural inputs, rather than of conscious management decisions (Tschakert and Tappan, 2004).

Reversing soil fertility decline will be key in sustaining agricultural production in Senegal. The importance of organic residue management, fallow-crop rotations, manure applications and planting of $N_2$-fixing trees such as *F. albida* for soil fertility improvement and carbon sequestration have been stressed by other researchers (Ganry et al., 2001; Manlay et al., 2000; Piéri, 1992; Tschakert and Tappan, 2004). Like many other trees, *F. albida* forms a symbiosis with arbuscular mycorrhizal fungi (AMF) (Dalpé et al., 2000). Symbiotic AMF produce an extensive mycelial network that may account for up to 25% of total soil microbial biomass (Olsson et al., 1999). These mycelia mobilize P and other essential nutrients, which improves plant nutrition and soil fertility. Furthermore, AMF produce large amounts of glomalin, a glycoprotein resilient to degradation that contributes importantly to the soil organic carbon (C) pool (Rillig, 2004; Rosier et al., 2006). As AMF derive their C and energy from their host plant, they can be considered as plant-derived soil C builders (Nakano et al., 1999). In this context, we hypothesize that trees and their associated AMF can increase the soil C and extractable nutrient concentrations directly by stimulating primary production, which increases C inputs from dead roots, leaves and root exudates, and indirectly by fostering the formation of AMF mycelia.

The objective of this work was therefore to evaluate what effect trees might have on AMF and soil fertility on smallholder farms in Senegal. The study involved semi-formal interviews, soil sampling and a tree survey with 22 Serer farmers owning 60 fields in the rural communities of Palmarin and Fimela, Senegal.

## 2. Materials and methods

### 2.1. Study area

The study involved three Serer villages in the Department of Fatick, approximately 150 km south of Dakar near the town of Joal-Fadiout, Senegal (Fig. 1). Palmarin Ngallou is located in the rural community of Palmarin (14°1′N, 16°46′W), while Samba Dia and Baboucar are both in the rural community of Fimela (14°8′N, 16°40′W). The climate in this area is Sudanian, with 500–700 mm of rainfall each year during the rainy season (July–October), whereby episodic droughts causing crop failure occur (Tappan et al., 2004). Mean monthly temperatures range from 17 °C in January to 27 °C in July (Institut de Recherche et Développement, 2004). The topography of the study area is rolling, with a succession of cropped valleys and pastoral plateaus. Soils are ferruginous tropical and ferralitic (Ferric Lixisols and Fluvisols; Khouma, 1998) and the vegetation consists of agricultural parklands, with trees such as the Ana tree

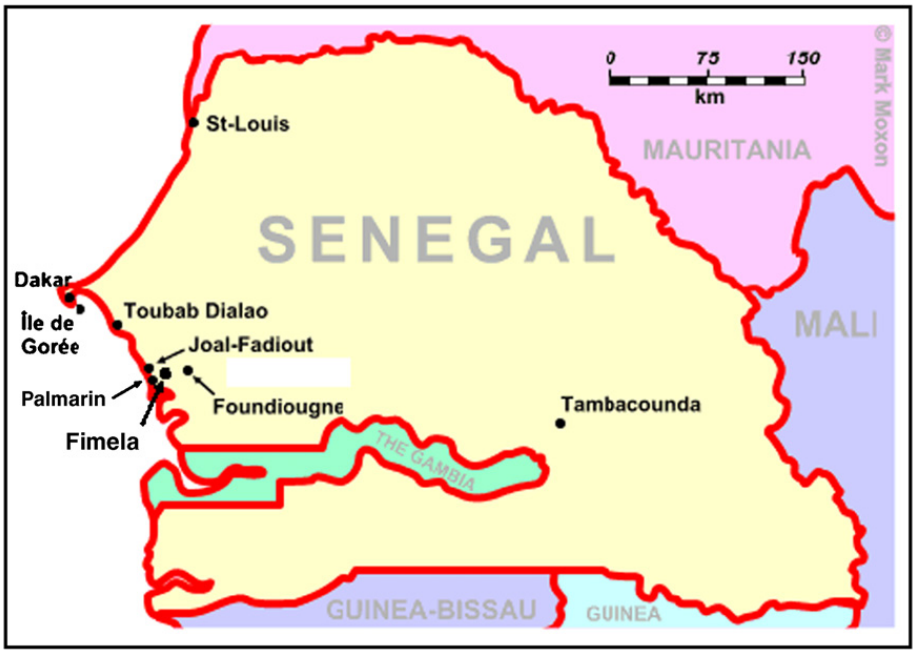


Fig. 1. Location of the rural communities of Palmarin and Fimela, Department of Fatick, Senegal. Source: http://www.moxon.net/senegal/index.html.

(*F. albida*, syn. *A. albida*), African baobab (*Adansonia digitata*), various wild ficus species, and pamyra palm (*Borassus aethiopum*) in cultivated fields.

## 2.2. Data collection

### 2.2.1. Interviews and tree survey

Interviews were conducted as oriented discussions with 22 farmers who resided in the village of Palmarin Ngallou, but cultivated 60 fields (0.5–2 ha) in both rural communities (Palmarin and Fimela). The questions referred to fertilizer strategies, field locations, crop rotations, environmental issues and the farmer's perception of family involvement in agricultural activities. In addition to these qualitative data, trees in each field were counted and tree species were identified.

### 2.2.2. Soil sampling and analysis

Soil samples were taken from the 0–5 cm depth, which generally has larger soil microbial communities and more nutrients than deeper soil layers, from the 60 cropped fields covered by the survey during the period 11 August to 5 September 2002. Each sample consisted of five cores taken with a soil auger (2 cm internal diameter), collected from random locations across the field and mixed to generate a composite soil sample for the field. Soils were air-dried in Senegal before being transported to Canada for analysis. Soil pH ($H_2O$) was analyzed using a 1:2 soil:solution ratio (Hendershot et al., 1993). Soil organic matter (SOM) content was determined by loss on ignition at 360 °C for 4 h (Schulte et al., 1991). Soils were extracted with Bray-1 solution at a soil:solution ratio of 1:7 (Bray and Kurtz, 1945), then the P concentration in Bray-1 extracts was analyzed colorimetrically on a Lachat Quik-Chem AE flow-injection autoanalyzer (Lachat Instruments, Milwaukee, WI, USA). In the same extracts, the K, Ca, Fe and Al concentrations were determined by atomic absorption spectrometry.

Dissolved C, N and P in soils were analyzed using the method of Houba et al. (2000). About 4 g of air-dried soil was extracted with 40 mL of 0.01 M $CaCl_2$ by shaking for 2 h at 20 °C with a horizontal shaker and filtered through Fisherbrand P2 filter paper (fine porosity, slow flow rate). The dissolved organic carbon (DOC) concentration was determined using a Shimadzu TOC-V analyzer (Shimadzu Corporation, Kyoto, Japan). Total dissolved N (TDN) was determined by digesting 4 mL of the $CaCl_2$ extract with 6 mL of alkaline persulfate solution (autoclaved at 121 °C for 1 h; Williams et al., 1995). The $NO_3$–N concentration in digested and undigested $CaCl_2$ extracts was determined by the cadmium reduction–diazotization method on a Lachat Quik-Chem AE flow-injection autoanalyzer (Lachat Instruments, Milwaukee, WI, USA). Dissolved organic N (DON) was calculated as the difference between $NO_3$–N concentrations in digested and undigested $CaCl_2$ extracts. The dissolved inorganic P (DIP) concentration was measured on a microplate system using the ammonium molybdate–malachite green assay (D'Angelo et al., 2001; Jeannotte et al., 2004).

The presence of AMF was assessed by measuring the concentration of a glycoprotein produced by these fungi that is relatively stable and retained in soils much longer (up to several years) than the original AMF hyphae (turnover time of days to weeks) (Rillig et al., 2003). Thus, glomalin was considered a marker of short- to long-term history of mycorrhizal fungi presence in the soils. Extraction of glomalin from soils, quantification of proteins in the corresponding soil extracts and detection of the immunoreactive glomalin were carried out as described by Wright and Upadhyaya (1996, 1998). About 1 g of air-dried soil was mixed with 8 mL of 20 mM citrate buffer (pH 7.0) and autoclaved at 121 °C for 1 h. The supernatant was collected after centrifuging the samples at 7800 $g$ for 15 min. Bradford-reactive soil protein (BRSP; μg protein $g^{-1}$ soil) in the supernatant was determined by the Bradford dye-binding assay with bovine serum albumin as the standard. The immunoreactivity (specificity) of the proteins was determined by an ELISA using the monoclonal antibody MAb32B11. The percentage of immunoreactive glomalin (IRG) was calculated as

$$\mathrm{IRG} = \left(\frac{\mathrm{IRSP}}{\mathrm{BRSP}}\right) \times 100\% \tag{1}$$

where IRSP is the immunoreactive soil protein concentration (μg protein $g^{-1}$ soil) according to Rillig (2004).

### 2.3. Statistical analysis

Descriptive statistics were calculated, including the minimum, maximum, mean and variance associated with each soil parameter by rural community ($n = 29$ fields in Palmarin and $n = 31$ fields in Fimela). Pairwise $t$-tests, using the Bonferroni test of probabilities, were used to compare the mean values reported for fields in Palmarin and Fimela. These calculations were performed with SYSTAT, version 10 (Systat Software Inc., Richmond, CA, USA).

Exploratory path analysis was used to determine the causal relationships between trees, AMF and soil parameters. Path analysis is a structural equation modeling technique that partitions correlations into direct and indirect effects. As such, it can be used to confirm or refute conceptual models describing mechanistic processes when model variables are intercorrelated (Hatcher, 1994). The correlation matrix for path analysis was generated using a normalized dataset (pooled data from both rural communities, $n = 60$) with the correlation procedure (PROC CORR) of SAS statistical software (SAS System 9.1, SAS Institute Inc., Cary, NC, USA). To avoid multicollinearity, we removed predictor variables with a variance inflation factor greater than 3. Path coefficients, their significance level and the fit of the structural model were calculated using the CALIS procedure, designed for the analysis of covariance structure models, in SAS. The path coefficients correspond to the standardized partial regression coefficients. We used the Goodness-of-Fit Index (GFI), the Normed Fit Index (NFI) and the $\chi^2$ statistic as indices of the model fit. When GFI and NFI were greater than 0.9 and the $\chi^2$ statistic was not significant, the predicted covariance matrix was considered to be in good agreement with the observed covariance structure in the data (Hatcher, 1994; Schumacker and Lomax, 2004).

## 3. Results

Most of the smallholder farmers in this study cultivated three or four fields, and field size ranged from 0.5 to 2.0 ha. The total area cultivated was 33.5 ha in Palmarin and 38 ha in Fimela. During the period 1999–2002, smallholder farmers grew millet, cowpea (*Vigna unguiculata* (L.) Walp.), peanut (*Arachis hypogaea* L.), sorghum (*Sorghum bicolour* (L.) Moench), maize (*Zea mays* L.) and roselle (*Hibiscus sabdariffa* var. *altissima* Wester). In 2002, the most important crop was millet, grown in 26 of the 60 fields studied. Cowpea and peanut were grown on 27% of the cultivated land, and 7% of land was left fallow. Only 32% of the fields received fertilizer, and the most common fertilizer source was cow manure (applied to 12 fields), followed by fish byproducts (4 fields), urea (2 fields) and phosphate fertilizer (1 field). Although fertilizer use was recorded, the quantities of fertilizer applied to each field were not known.

Soils were slightly acidic (on average pH = 6.1) and contained about 1% SOM (Table 1). Although most soil fertility indicators did not differ between rural communities, the fields in Palmarin had significantly ($P<0.05$) greater soil pH, Bray-1 P, extractable Al, DOC and DIP concentrations than fields in Fimela (Table 1). In soils from these rural communities, the DIP concentration was about 10-fold lower, but significantly correlated ($r = 0.71$, $P<0.001$, $n = 60$) with the Bray-1 P concentration. Tree density (number of trees $ha^{-1}$) was about seven times greater in Palmarin than in Fimela, and the diversity of trees was also greater in Palmarin (18 species) than in Fimela (13 species) (Tables 1 and 2).

The model with the best fit (GFI = 0.9868, NFI = 0.9810 and non-significant $\chi^2$, $P = 0.817$) was expressed in a path diagram (Fig. 2). This model revealed a direct and significant ($P<0.05$) impact of trees and soil mineralogy (represented by Bray-1 extractable Ca) on SOM and pH (Fig. 2). Further, pH and extractable Ca had a direct, positive effect on the soluble P (DIP) concentration (Table 3, Fig. 2). The results of the path analysis also suggested that the SOM pool had direct and indirect effects on the $NO_3$–N concentration and AMF, as determined from glomalin analysis (Table 3, Fig. 2).

## 4. Discussion

### 4.1. Cropping practices on smallholder farms

About 44% of the cultivated land was dedicated to millet production, which reflects the importance of this crop as a staple in the Serer diet (Pélissier, 1966). Cowpea and peanut were grown as cash crops. A few fields were left fallow, because they reportedly had given disappointing yields in previous years or because farmers were too busy to cultivate them. Trends in fallowing and fertilizer use obtained from the survey were consistent with agricultural practices in this region during in the 1990s (Tappan et al., 2004; Tschakert and

Table 1
Differences in soil properties and trees cultivated on smallholder farms in the rural communities of Palmarin and Fimela, Department of Fatick, Senegal

| Parameters[a] | Units | Palmarin | | Fimela | | *t*-test |
|---|---|---|---|---|---|---|
| | | $n$[b] | Mean (±S.E.M.)[c] | $n$ | Mean (±S.E.M.) | $P$-values[d] |
| pH | | 29 | 6.4 (±0.1) | 31 | 5.8 (±0.1) | <0.01** |
| SOM | $g\,kg^{-1}$ | 29 | 11 (±0.8) | 31 | 8.6 (±0.4) | ns |
| Bray-1 P | $mg\,kg^{-1}$ | 29 | 27 (±3.4) | 30 | 8.5 (±1.4) | <0.001*** |
| Bray-1 K | $mg\,kg^{-1}$ | 28 | 71 (±9.0) | 30 | 59 (±7.4) | ns |
| Bray-1 Ca | $mg\,kg^{-1}$ | 29 | 440 (±24) | 31 | 361 (±19) | ns |
| Bray-1 Fe | $mg\,kg^{-1}$ | 29 | 10 (±1.1) | 31 | 6.8 (±0.7) | ns |
| Bray-1 Al | $mg\,kg^{-1}$ | 27 | 92 (±3.1) | 27 | 73 (±3.0) | <0.01** |
| DOC | $mg\,kg^{-1}$ | 29 | 67 (±4.3) | 31 | 37 (±1.3) | <0.001*** |
| $NO_3$–N | $mg\,kg^{-1}$ | 29 | 16 (±1.8) | 31 | 15 (±1.5) | ns |
| DON | $mg\,kg^{-1}$ | 29 | 12 (±0.7) | 31 | 11 (±0.9) | ns |
| DIP | $mg\,kg^{-1}$ | 29 | 2.5 (±0.4) | 31 | 0.63 (±0.2) | <0.01** |
| BRSP | $mg\,kg^{-1}$ | 29 | 416 (±14) | 31 | 433 (±21) | ns |
| IRSP | $mg\,kg^{-1}$ | 29 | 10 (±2.0) | 31 | 19 (±3.8) | ns |
| IRG | | 29 | 2.4 (±0.5) | 31 | 4.7 (±1.1) | ns |
| Tree density | Trees $ha^{-1}$ | 29 | 14 (±3) | 31 | 2 (±0.4) | <0.05* |
| No. of tree species per field | | 29 | 3.6 (±0.4) | 31 | 1.4 (±0.2) | <0.001*** |

[a] *Abbreviations*: SOM, soil organic matter; DOC, dissolved organic carbon; DON, dissolved organic nitrogen; DIP, dissolved inorganic phosphorus; BRSP, Bradford-reactive soil protein; IRSP, immunoreactive soil protein; IRG, percent immunoreactive glomalin.

[b] $n$, number of observations.

[c] S.E.M., standard error of the mean.

[d] Bonferroni test of probabilities: $^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$.

Table 2
Tree species diversity on smallholder farms in the rural communities of Palmarin and Fimela, Department of Fatick, Senegal

| Trees species | Palmarin | | | | Fimela | | | |
|---|---|---|---|---|---|---|---|---|
| | *n* | Min | Max | Total | *n* | Min | Max | Total |
| *Acacia sieberiana* | 29 | 0 | 5 | 8 | 31 | 0 | 1 | 1 |
| *Adansonia digitata* | 29 | 0 | 8 | 47 | 31 | 0 | 1 | 7 |
| *Borassus aethiopum* | 29 | 0 | 11 | 30 | 31 | 0 | 4 | 10 |
| *Ceiba pentandra* | 29 | 0 | 1 | 1 | 31 | 0 | 0 | 0 |
| *Celtis integrifolia* | 29 | 0 | 3 | 6 | 31 | 0 | 1 | 1 |
| *Clerondendron aculeatum* | 29 | 0 | 1 | 1 | 31 | 0 | 0 | 0 |
| *Croton scarciesii* | 29 | 0 | 0 | 0 | 31 | 0 | 1 | 1 |
| *Detarium senegalense* | 29 | 0 | 6 | 23 | 31 | 0 | 0 | 0 |
| *Elaeis guineensis* | 29 | 0 | 40 | 85 | 31 | 0 | 0 | 0 |
| *Euphorbia* sp. | 25 | 0 | 5 | 5 | 31 | 0 | 0 | 0 |
| *Faidherbia albida* | 29 | 0 | 12 | 49 | 31 | 0 | 10 | 39 |
| *Ficus asperifolia* | 29 | 0 | 3 | 9 | 31 | 0 | 1 | 5 |
| *Ficus vogelii* | 29 | 0 | 1 | 5 | 31 | 0 | 0 | 0 |
| *Mangifera indica* | 29 | 0 | 0 | 0 | 31 | 0 | 2 | 4 |
| *Maytenus senegalensis* | 29 | 0 | 1 | 1 | 31 | 0 | 0 | 0 |
| *Microdesmis puberula* | 29 | 0 | 0 | 0 | 31 | 0 | 2 | 3 |
| *Parinari macrophylla* | 29 | 0 | 18 | 40 | 31 | 0 | 0 | 0 |
| *Pavetta oblongifolia* | 29 | 0 | 0 | 0 | 31 | 0 | 1 | 1 |
| *Piliostigma reticalatum* | 29 | 0 | 20 | 21 | 31 | 0 | 1 | 1 |
| *Sclerocarya birrea* | 29 | 0 | 3 | 4 | 31 | 0 | 0 | 0 |
| *Tamarinus indica* | 29 | 0 | 0 | 0 | 31 | 0 | 2 | 2 |
| *Ziziphus mauritiania* | 29 | 0 | 6 | 18 | 31 | 0 | 1 | 1 |
| *Ziziphus mucronata* | 29 | 0 | 4 | 10 | 31 | 0 | 0 | 0 |
| Sum of all trees counted | | | | 363 | | | | 76 |

Tappan, 2004). Remote sensing data indicated that virtually all arable land in the Saloum Agricultural Eco-Region, where this study took place, was cultivated and there was little use of fallow or soil conservation practices during the 1990s (Tappan et al., 2004). In the Serer village of Ngodjilème, in the West-Central Agricultural Region, the fallow area declined from 21% to 2% during the period 1968–1999 (Tschakert and Tappan, 2004). The reduction in fallow land in these studies was attributed to demographic pressures that increased the need to cultivate land and produce crops for human and animal consumption. Demographic pressure may explain why only 7% of fields were fallow in 2002, but another reason is that abundant rainfall during the period 1998–2001 and good crop yields from 1999 to 2001 could have enticed farmers to plant crops rather than leave the land fallow (FAO, 2002).

In addition to fallowing, smallholder farmers in Senegal rely on manure, compost, household waste and mineral fertilizers to maintain soil fertility (Manlay et al., 2004). In the West–Central Agricultural Region, smallholder farmers applied between 0 and 4000 kg manure $ha^{-1}$ and from 0 to 300 kg mineral fertilizer $ha^{-1}$ (Tschakert and Tappan, 2004). Smallholder farmers in the Casamance Region did not fertilize fields that were regularly fallowed and tended to reserve the highest manure inputs for continuously cropped fields (Manlay et al., 2004). It is not possible to comment on the quantity of fertilizer applied to fields in this study because the data were not available, but continuous cultivation without fertilizer inputs is likely to deplete soil C, N and P pools (Manlay et al., 2004).

### 4.2. Soils and trees

Soils containing less than 12 mg Bray-1 P $kg^{-1}$ are considered low in P and those containing 13–25 mg Bray-1 P $kg^{-1}$ have a medium P status (Havlin et al., 2005). According to this definition, Fimela fields were low and Palmarin fields were medium in P fertility. These values are similar to those from other studies on West

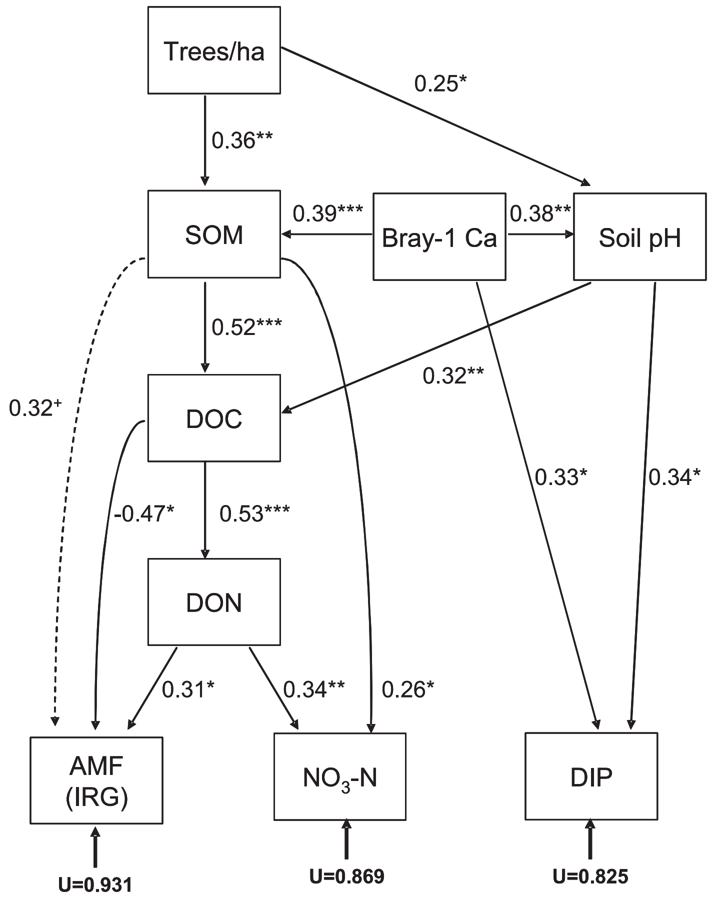


Fig. 2. Exploratory path model describing hypothesized causal relationships between trees, soil fertility and arbuscular mycorrhizal fungi (AMF). Abbreviations are described in Table 1. Single-headed arrows indicate a hypothesized direct causal relationship. For each effect path, standardized path coefficients are given (significant at $^{+}P<0.1$, $^{*}P<0.05$, $^{**}P<0.01$ and $^{***}P<0.001$). Marginally significant paths coefficients are indicated with a dotted line. The residual variable (U) indicates the contribution of all unmeasured or unknown factors to the response variables.

Table 3
Direct and indirect effects, and simple correlation coefficients describing the relationships between soil variables, soil fertility indicators and arbuscular mycorrhizal fungi (pooled data from smallholder farms in Senegal, $n = 60$)

| Variable[a] | Direct effect | Indirect effect | Correlation coefficient ($r$) |
|---|---|---|---|
| Dissolved inorganic P (mg DIP $kg^{-1}$) | | | |
| PH | $0.34^{*}$ | NA[b] | $0.49^{***}$ |
| Bray-1 Ca | $0.33^{*}$ | NA | $0.48^{***}$ |
| $NO_3$–N (mg $NO_3$–N $kg^{-1}$) | | | |
| SOM | $0.26^{*}$ | 0.09 | $0.38^{**}$ |
| DON | $0.34^{**}$ | NA | $0.43^{***}$ |
| Arbuscular mycorrhizal fungi (IRG) | | | |
| SOM | $0.32^{+}$ | −0.16 | $0.11^{NS}$ |
| DOC | $-0.47^{*}$ | 0.16 | $-0.11^{NS}$ |
| DON | $0.31^{*}$ | NA | $0.16^{NS}$ |

The direct effects (standardized partial regression coefficients) and correlation coefficients were not significant (NS) or significant at $^{+}P<0.1$, $^{*}P<0.05$, $^{**}P<0.01$ and $^{***}P<0.001$.
[a]Same abbreviations as Table 1.
[b]NA: not applicable.

African soils (Doumbia et al., 1998; Manu et al., 1991). In Gambia, Peters (2000) reported average Bray-1 P levels of 7.4 mg P kg$^{-1}$ soil in peanut fields, 10 mg P kg$^{-1}$ in millet fields and 19 mg Bray-1 P kg$^{-1}$ in maize fields. The higher soil fertility in Palmarin may be related to fertilization, crop rotation, tree cultivation and other factors that remain to be quantified. Smallholder farmers perceived that yields were higher in Palmarin than in Fimela fields, but this should be confirmed by measuring crop yields in these fields.

The IRSP concentration of 10–19 μg protein g$^{-1}$ and the IRG of 2.4–4.7% measured in this study fall within the range of published data for glomalin in soils from semi-arid rangelands in New Mexico (Bird et al., 2002), drylands in Texas (Wright and Upadhyaya, 1998) and semi-arid Mediterranean steppes (Rillig et al., 2003). Most plants cultivated in the study area could support the AMF symbiosis, which is why glomalin was ubiquitous in all fields sampled. The data do not allow us to determine if glomalin was freshly deposited by AMF during the previous rainy season or whether it was part of a more resilient pool of soil proteins. Further work is needed to understand glomalin transformations and contributions to the soil organic C pool in West African soils.

The most striking difference between the Palmarin and Fimela rural communities was that fields in Palmarin had more trees and more different tree species than those in Fimela. African baobab (*A. digitata*), the Ana tree (*F. albida*), pamyra palm (*B. aethiopum*), two local fruits trees (*Parinari macrophylla* and *Detarium senegalense*), oil palm (*Elaeis guineensis*) and the wild ficus species *Ficus asperifolia* were among the dominant species (see Table 2). A few trees may be remnants of the ancient woodland that once blanketed the region (Tappan et al., 2004), but most were probably planted for food, fuel, medicinal purposes and shade. The spatial pattern of trees in these rural communities (high tree density around Palmarin Ngallou, where the smallholder farmers resided, and low tree density in the cultivated fields that were distant from the primary residence), is consistent with the report of Tschakert and Tappan (2004). In the West-Central Agricultural Region, they found an unwritten code that included the protection of field trees, particularly *F. albida* and prevented tree cutting inside the residential village. However, trees farther from the residential village are more vulnerable to exploitation because farmer's activities are less constrained by social norms (Tschakert and Tappan, 2004). Similar codes of tree protection were reported for other Serer villages in the area (Garin et al., 1990; Lericollais and Faye, 1994).

Planting trees is perceived by Serer farmers to be the most direct way to improve soil fertility (Tschakert and Tappan, 2004). The hypothesis proposed at the outset of this study was that the tree–AMF association would increase the soil C pool and extractable nutrient concentrations, but this was not supported by the path analysis model (Fig. 2). Instead, the results suggested that trees and soil mineralogy had a direct effect on pH and the SOM pool. Further, pH and extractable Ca had a direct, positive effect on the soluble P (DIP) concentration, which was strongly correlated with Bray-1 P. In acidic soils, more soluble P is released into the soil solution as the pH increases, reaching a maximum around pH = 6.5 (Havlin et al., 2005). The relationship between the SOM pool and the soil $NO_3$–N concentration is consistent with general knowledge that mineralization and nitrification processes are affected by the quantity of SOM and the availability of readily mineralizable organic N compounds, represented by DON (Havlin et al., 2005). The relationships between SOM, DOC, DON and AMF in the path diagram are less clear, but this may be due to the ubiquitous distribution of the glomalin proteins in the fields studied. The path analysis model suggests that growing more trees could increase the SOM pool and soil pH, which would, in turn, increase the amount of plant-available N and P.

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