
PART

I

ORGANIC·STATUS·OF
AGROECOSYSTEMS·OF
A·WEST·AFRICAN·SAVANNA

THE PLOT SCALE

CHAPTER 1.

CARBON, NITROGEN AND PHOSPHORUS

ALLOCATION IN AGRO-ECOSYSTEMS

OF A WEST AFRICAN SAVANNA.

II. THE PLANT COMPONENT

UNDER SEMI-PERMANENT CULTIVATION



15- year old fallow in Sare Yorobana

Chapter 1. CARBON, NITROGEN & PHOSPHORUS ALLOCATION IN AGRO-ECOSYSTEMS OF A WEST AFRICAN SAVANNA - I. THE PLANT COMPONENT UNDER SEMI-PERMANENT CULTIVATION

Submitted to Agriculture Ecosystems & Environment

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ABSTRACT

Dry matter (DM), carbon (C), nitrogen (N) and phosphorus (P) allocation occurring in plant biomass under semi-permanent cultivation in savannas of southern Senegal was measured through a chronosequence including 25 groundnut crops and plots left to fallow for one to 26 years. The amounts in cropped plots amounted to 14.7 tDM, 5.5 tC, 106 kgN and 5.9 kgP per hectare. They increased to 48 tDM, 17.7 tC, 231 kgN and 19.6 kgP in fallow plots aged 1-9 years. A threshold was reached after 10 years of fallow. Beyond it biomasses remained steady. Older fallow plots stored 79.2 tDM, 29 tC, 333 kg N and 33.8 kgP. Highest increases in woody components were found during the very first year following crop abandonment, and were achieved at the expense of the herbaceous layer. Carbon and nutrient allocation to woody below-ground biomass occurred only later, as testified by adjustments to the logistic model, and by the evolution of the shoot:root ratio. Simulations indicated that massive nutrient losses occurred at clearing due to both burning and wood exportation.

Because storage in woody and herbaceous biomass remained steady in fallows aged more than 10 years, young fallows were found to have the most interesting productivity for wood and forage. However, because this productivity relies on the high resprouting capacity of local tree species, and because this capacity can be maintained only thanks to long breaks of fallow, improving the management of fallows, or substituting agroforestry techniques for them, should aim at preserving perennial rooting systems in the semi-permanent cultivation systems of West African savannas.

KEY WORDS

Plant biomass, Carbon, Nitrogen, Phosphorus, Root, Savanna, Senegal, Semi-permanent cultivation

1.1. INTRODUCTION

Favourable temperature and insolation allow high potential values of net primary productivity in the Tropics. However, corollary drawbacks such as weed encroachment, and pest and disease vitality, seriously impede the efficiency of tropical farming (Ruthenberg, 1971). In the West African savanna belt, other specific biophysical restrictions to crop and animal production are: erratic and seasonal rainfall, soil sensitiveness to erosion and poor nutrient status (Jones and Wild, 1975; Kowal and Kassam, 1978). Low availability of working power due to weak mechanisation, limited access to chemical inputs and common land tenure are the main human features, that all together with natural constraints, explain the local choices for diversified, labour-saving, and extensive schemes of crop and animal production (Ker, 1995). Apart from restricted areas of flooded agriculture, practices that sustained soil fertility in traditional farming systems were mainly organic. In most of the subregion, this was, and yet is, the aim of manuring, fallowing, mulching and composting to a lesser extent (Ruthenberg, 1971). These techniques have proved to be adapted to sparsely populated areas and have led to the widespread practice of ring management in African villages (Pélissier, 1966; Ruthenberg, 1971; Prudencio, 1993).

Three main rings are roughly distinguished (Figure 1.1):

- (1) the savanna or forest ring, that has never -at least not for several decades- been cultivated. Because this is the farthest ring from the village, integration to the farming system remains low, although it can provide wood and essential pasture during the wet season. Unlike the other rings, this area is usually not appropriated by the village,

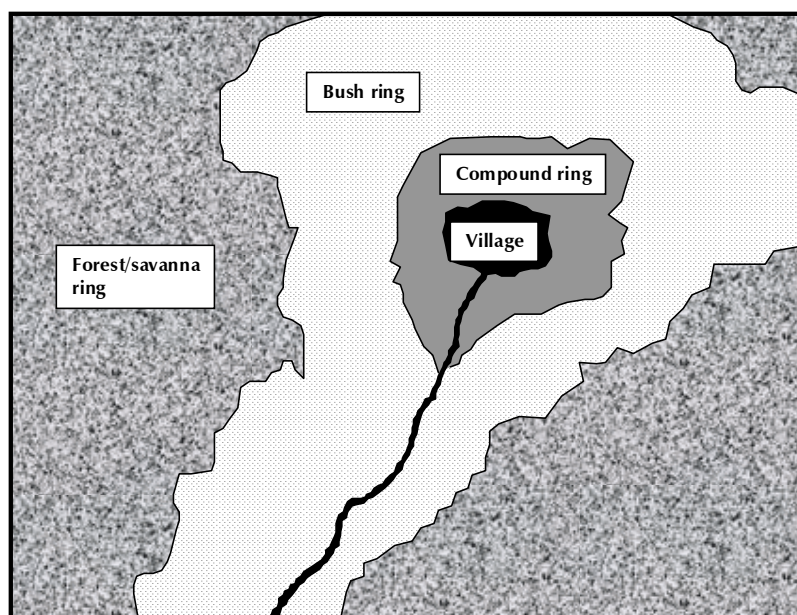


Figure 1.1 Simplified ring organisation of a village of the mixed-farming system of the West African savanna belt.

- (2) the bush ring, which consists of a mosaic of bush fields -mainly cash crops- and young to old fallows. Fertility is mainly sustained by fallowing. Fallow can also occur due to a shortage of working power or of crop seeds,
- (3) the compound ring, devoted to food crops. Intensified continuous cultivation is enabled by manuring (mostly during night corralling) and household waste inputs throughout the dry season.

Because of local and global reasons, there is a growing need to assess carbon, nitrogen and phosphorus storage in savanna agroecosystems of West Africa as related to soil characteristics and land management.

At a local scale, and for a few decades, rural population dynamics, land tenure politics and technical innovations have encouraged a shift in traditional practices. While the savanna ring has been almost vanishing, the bush ring area has dramatically shrunk because of growing needs for land, and for the benefit of continuous cultivation. Although this trend is not to be reversed soon, it is generally admitted that multi-purpose, improved fallows will keep playing a role in farming systems of savannas, while intensification in the compound ring will be maintained by better crop-livestock integration and agroforestry practices.

Most African agricultural policies implemented during the last 30 years have led to unsustainable and slow production increase due to incomplete knowledge about the ecological bases of tropical ecosystem fertility, especially in the savanna belt (Brown and Thomas, 1990). A better understanding of agro-ecological patterns of fertility conservation occurring in existing semi-permanent and continuous cropping systems in savanna is a prerequisite to the safe adoption of any technical innovation.

The hypothesis underlying our work is that this understanding mainly relies on the study of the organic matter-mediated cycles of carbon, nitrogen, and phosphorus. Special emphasis will be put on organic matter and carbon dynamics. In largely self-sufficient farming systems, indeed, organic matter supplies peasants with food and wood, and livestock with forage (Floret *et al.*, 1993). It is its proper management that ensures the sustainability of the agroecosystem too. In heavily leached sandy sub-Saharan soils, chemical, physical and biological soil properties hang on soil organic matter status (de Ridder and van Keulen, 1990). Nitrogen and phosphorus were also largely included in the present study, because these elements are the most limiting chemical factors to plant productivity in African savannas (Jones and Wild, 1975). Another reason for such consideration is that the nitrogen cycle is closely related to the organic matter cycle, and that it characterises the quality of carbon involved in the plant-soil system. Because the present work is an integral part of an attempt to assess current and future carbon stocks and fluxes at the scale of a village agroecosystem (Chapters 4 and 5), it also provides parameterised models of carbon dynamics in the main organic components of the agroecosystems of this savanna ecozone. The plant biomass produced under semi-permanent cultivation systems in West-African savannas does not only provide a valuable source of fibre and energy for farmers and their livestock. Because of the chemical poverty of local soils, soil fertility is closely related to the dynamics of the vegetation, which ensures the

safe accumulation of nutrients, drives soil nutrient availability to plants, and initiates patterns of energy redistribution to the soil biota (Perry *et al.*, 1989; Hendrix *et al.*, 1990).

On a more global perspective, land use changes in the tropics would have been responsible for nearly a fifth of the total release of anthropogenic carbon in the 1980s (Schimel, 1995). In Senegal, more than 40 % of carbon dioxide emissions stems from agriculture, land use changes and forests (Sokona, 1995). Reviews of Desanker *et al.* (1995) and Tiessen *et al.* (1998) emphasise the scarcity of carbon budget assessment in dry tropical ecosystems as compared to wetter zones, and the particular paucity of studies in Africa with regard to the work already achieved in other dry tropical regions of the world. Considering West African demographic and economic contexts, the control of greenhouse gas emissions may not become a priority as such for political leaders. But carbon sequestration in African smallholder agriculture is a key to sustainable intensification and recovery of farmers' wealth (Woomer *et al.*, 1998). Evaluating carbon sequestration potential of agro-ecosystems of the sub-region was thus another goal of our work.

This chapter is the first of a series of three, aimed at assessing carbon (C), nitrogen (N) and phosphorus (P) allocation in the bush and compound rings of a mixed-farming system of southern Senegal. The present part deals with C, N and P allocation in plant biomass during the crop-fallow cycle usually happening in the bush ring, while soil allocation is studied in Chapter 2. Storage of C, N and P in plant biomass and soil under continuous cultivation is reported in Chapter 3.

In this study we (a) describe recovery patterns of dry matter (DM), C, N and P biotic allocation and study hierarchical relations between organic components during fallow (b) define temporal thresholds of evolution for DM, C, N and P in the components of plant biomass (c) evaluate the fate of above-ground plant biomass and related nutrients after conversion to crop.

1.2. METHODS

1.2.1. Site characteristics

The study has been led between 1993 and 1997 in High Casamance, southern Senegal. Crop and fallow plots were investigated in the village of Sare Yorobana (12°49'N – 14°53'W). The climate is Sudanian, tropical dry. Annual rainfall ranged between 570 and 1320 mm (mean: 960 mm) during the last 20 years and occurred from May to October (Figure 1.2); temperature averaged 28 C (Service de la Météorologie Nationale, station of Kolda). Mean annual potential evapotranspiration was 1570 mm between 1977 and 1988 (Dacosta, 1989).

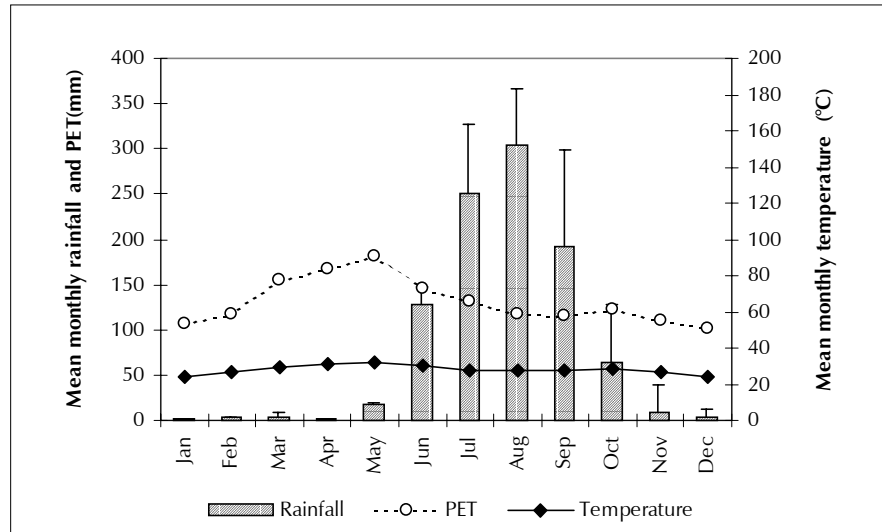


Figure 1.2 Monthly patterns of rainfall, potential evapotranspiration and temperature at the station of Kolda, 1978-1997. Vertical bars stand for standard error. PET: potential evapotranspiration. See data in Appendix 3.

Ring-like, compound-centred management of the village individualises three main land use systems or units along the typical, smooth toposequence:

- (1) The up-slope plateau. It is still covered with vast areas of “woodlands with a well developed tree stratum and shrubby undergrowth” (de Wolf, 1998), savanna and old fallows. Resprouting Combretaceae are the major component of woody vegetation. In the study site four woody species dominate, amounting to 70 % of woody above-ground biomass (AGB): *Combretum geitonophyllum* Diels, *Combretum glutinosum* Perr., *Piliostigma thonningii* (Sch.) Miln.-Redh and *Terminalia macroptera* G. et Perr.. Bush fields at the edge of the plateau are devoted to the cropping of a groundnut (*Arachis hypogaea* L.) local cultivar of the Virginia type, usually in rotation with millet if manured, but mostly with short fallow rotation. Cotton (*Gossypium hirsutum* L.), the main other cash crop, is also to be found in this unit. The soil is sandy, ferruginous (Baldensperger *et al.*, 1967), and is classified as a ferric Lixisol (FAO, 1998b). A more detailed description can be found in Chapter 2 and in Appendix 4. This unit encompasses the forest/savanna and most of the bush rings. All sampled plots, except three, belong to the plateau (see Methods).
- (2) the mid-slope glacis, sharing soils similar to the plateau (haplic Lixisols). It bears the compound ring, and thus continuous cultivation crops with cereals (pearl millet -*Pennisetum glaucum* L.; maize -*Zea mays* L.; sorghum -*Sorghum bicolor* L. Moench).
- (3) the lowland, devoted to rice and palm plantation, with soils being Gleysol (FAO, 1998b) (see Chapter 3 for more details).

Sedentary Fulani herdsmen have adopted a diversified agriculture (rainfed and flooded cereals, groundnut and cotton cash crops) closely associated with extensive livestock raising. In the bush ring, the rotation of

groundnut, fallow and sometimes millet is quite unpredictable. The traditional pattern of cropping in this ring is as follows. In practice, plant biomass produced during fallowing is either exported for wood and forage use, or burnt during uncontrolled fires. Massive disappearance of plant biomass happens at clearing, due to on-site burning and wood removal; only rooting systems are saved (Floret *et al.*, 1993). Traditional hand clearing can be labour-intensive, but woody stumps allowing regular resprouting are maintained several years before they die (Bohringer *et al.*, 1996). Clearing of old fallows or savanna is usually followed by two to four years of continuous cropping implying the biennial rotation of groundnut with cereals (millet, sorghum). After the rapid loss of the initial fertility (four to five years), continuous cultivation can be maintained a few more years if proper manuring is carried out prior to cereal cropping. However, food needs are usually met with crops from the compound ring, and livestock availability is often insufficient, so that the biennial rotation of groundnut with fallow occurs rapidly, if not straight away, after clearing. The rotation is maintained as long as soil fertility and low weed competition allow good yields. The field is then returned to fallow for several years, the length of fallow depending on soil properties, labour availability or land tenure factors.

1.2.2. Sampling schemes

A time-saving, synchronic method was adopted: neighbouring crop and fallow plots with different ages can be considered as the representatives of the same plot through the succession, assuming that they share the same initial soil properties and management history (Sanchez, 1987).

The sampling was done at the onset of the dry season, very close to peak plant above-ground biomass (AGB).

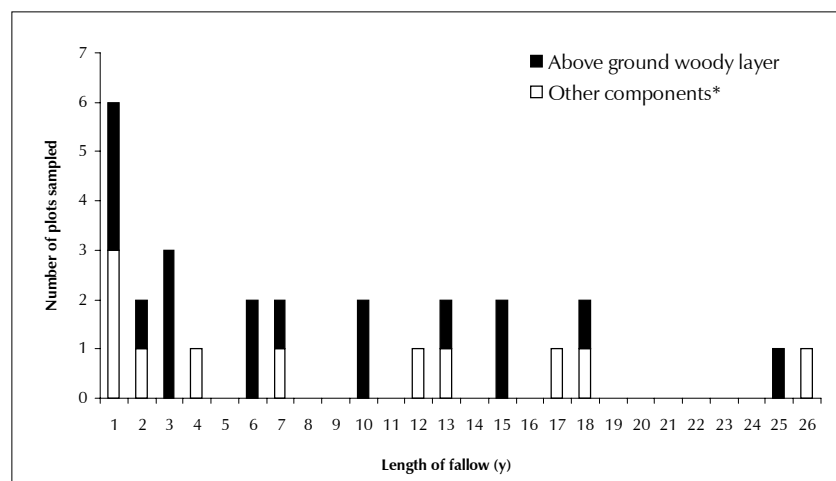


Figure 1.3 Distribution of the length of fallow among the 28 sampled plots of fallow.
* including soil (see Chapter 2).

Due to vegetation patterns, two designs were adopted, depending on land use:

- (1) Fallow plots (FA), aged 1-26 years (Figure 1.3): woody AGB was estimated on 17 plots (three 900 m² square-like subplots for each). Woody AGB (trunk –any branch with a diameter above 4 cm-, twig and leaf) and stump biomass (in fallows aged more than 4 years) were estimated using a regression relationship based on the tree diameter at breast height, that is 1.3 m (Table 1.1) (Kairé, 1999). Other variables were sampled every meter in a 0.5-m² parallelepiped, along a 20-m long and 0.5-m wide transect, in 11 plots different from the previous ones but all located on the plateau (except plot FA01a, settled on the upper glaxis) (Appendix 1). Herbaceous layer was harvested, comprising live and dead (but standing) plant biomass. Litter was picked as the figured A0 organic layer ($\varnothing > 2\text{mm}$). Fine roots were sampled with a core auger (\varnothing : 5.6 cm) in 10-cm increments. On-field manual separation from soil excavated down to a 40-cm depth was used for coarse roots recovery, because core sampling is not accurate for roots coarser than 2 mm. In fallows aged four years or less, stumps were pulled out together with coarse roots.

Table 1.1 Regression coefficients used for woody biomass estimate for the four main species found in Sare Yorobana.

Species	Component	a	b	R ²
Combretum geitonophyllum	above ground biomass	0.283	2.17	0.97
	- trunk	0.103	2.44	0.97
	- twig	0.0947	2.15	0.96
	- leaf	0.0682	1.74	0.94
	stump	0.205	1.63	0.89
Combretum glutinosum	above ground biomass	0.149	2.33	0.98
	- trunk	0.0965	2.43	0.96
	- twig	0.0782	2.16	0.91
	- leaf	0.0676	1.99	0.94
	stump	0.175	1.78	0.80
Piliostigma thonningii	above ground biomass	0.157	2.27	0.97
	- trunk	0.0898	2.29	0.94
	- twig	0.0785	1.99	0.96
	- leaf	0.0554	1.79	0.89
	stump	0.149	1.66	0.89
Terminalia macroptera	above ground biomass	0.0979	2.40	0.96
	- trunk	0.0966	2.52	0.97
	- twig	0.0626	2.38	0.97
	- leaf	0.035	2.02	0.92
	stump	0.155	1.69	0.92
Others	above ground biomass	0.172	2.29	
	- trunk	0.0965	2.42	
	- twig	0.0785	2.17	
	- leaf	0.0566	1.89	
	stump	0.1710	1.69	

Model: biomass (in kgDM) = $a \cdot D^b$ with D the diameter -in cm- at breast height

Number of replicates: above-ground biomass: $n=40$; trunk, twig, leaf and stump: $n=15$.

Other species: parameters estimated as the mean of the parameters of the four main species.

Derived from Kairé (1999).

- (2) Cropped groundnut plots (coded as GN): six fields that had borne groundnut in a biennial rotation with fallow -or sometimes millet- for four to 15 years, and that had never been chemically fertilised, were chosen up-slope. Four lay on the plateau, two on the upper glaxis (GN04 and GN06). In each of them, four 16-m² square subplots were randomly defined. In each square, vegetation was cut for plant biomass assessment, with a distinction made between woody (stump regrowth) and herbaceous (weed and groundnut) layers. Litter biomass was nearly negligible, and it was not sampled. Fine roots were cored at each subplot's corner. Coarse root biomass was estimated with a regression relationship, established in fallows. This relation proved to be satisfactory to link coarse root biomass as measured by full excavation (a) to that measured by the coring technique (b): $a=1.73 \cdot b + 2.95$ (in tDM ha⁻¹); $R^2=0.6$; $p\{F_{obs} > F_{th}\} < 0.05$; $n=9$ (Appendix 5). Three out of the six groundnut fields (GN02, GN03 and GN04) investigated in 1996 were re-sampled in 1997 as one-year old fallows; in these plots stump

biomass was assumed (and thus probably slightly over-evaluated) to be that measured in the same (uncropped) plots in 1996.

In all plots, below-ground plant biomass (BGB) was sampled down to a 40-cm depth. This limit was chosen according to local unpublished observations and to other published works (Chopart, 1980; Tomlinson *et al.*, 1998). They indicate a very weak root activity below a 40-cm depth in soils of dry tropical West Africa.

1.2.3. Plant analyses

Stumps and coarse roots were hand washed and sorted according to their diameter ([2-5], [5-10], >10 mm). Fine roots were recovered from soil after hydro-pneumatic elutriation above a 1-mm sieve (Webb, 1995). All plant samples were oven-dried at 70 °C to constant weight for dry matter (DM) content determination. Samples were pooled and one analysis of each component was made for each plot. C content was determined after dichromate oxidation, N with the Kjeldahl method; P was measured on ashes. All methods are fully described in Page *et al.* (1989). C, N and P storage values were obtained by directly combining DM stock values and chemical content of plant biomass (Table 1.1 and Table 1.2a,b; see Kairé, 1999 for the detailed calculation of C, N and P amounts in woody biomass).

1.2.4. Study of the fate of post-fallow above-ground biomass

The fate of woody AGB (burnt on site or brought back to the compound) at clearing hangs upon branch diameter. Enquiries among farmers indicated that 4 cm was the threshold beyond which tree biomass was exported for wood need, while smaller twigs and leaves (available biomass for burning or ABB) were burnt on site. Combustion efficiency was not measured, and hangs upon local practices. Taking into account the works of Stromgaard (1985) and Fearnside and Barbosa (1998), two scenarios were considered, depending on the burning efficiency (90 and 50 %) of remaining plant biomass. They were applied to two hypothetical fallow plots: a young (aged less than 10 years) and an old fallow plots (aged 10 years or more); woody AGB of these plots was derived from the means computed in Table 1.6.

1.2.5. Data analyses

In sub-humid savannas, plants compete more for nutrients than for water, and fire yearly destroys most of the grass layer; this is why the dynamic of woody plant is not driven much by competition with the grass layer (Walker, 1985). We therefore hypothesised that temporal dynamics of plant dry matter and related nutrient storage could be adjusted to the logistic model. This model accounts well for population dynamics with limited nutrient availability (Pavé, 1994). Mathematical expression is:

$$S(t) = \frac{K}{1 + \frac{(K - S_0)}{S_0} \cdot e^{-r \cdot t}}$$

where S_0 is the value of the stock at $t=0$ and $K = \lim S$ when $t \rightarrow +\infty$.

A slightly modified generalised form of the model had to be adopted for two reasons:

- (1) Tree dynamics at crop abandonment is all the more autonomous with regard to other living functional groups, because it relies on stump re-growth and not just seedling. Thus, maximum increase of plant biomass can occur during the first years of fallow.
- (2) We also wanted to test the two following hypotheses (a) in local savannas, grass biomass is controlled by competition for light with trees (Akpo, 1998) and could thus be modelled as a simple linear function of tree biomass (b) tree and grass layers contributed equally to fine root biomass with respect to their biomass, and thus fine root biomass could be described as the sum of two linear functions of woody and herbaceous AGB.

The model finally tested was:

$$S(t) = \frac{a \cdot K}{1 + \frac{(K - S_0)}{S_0} \cdot e^{-r \cdot t}} + b$$

Including values measured in crop plots for model parameterisation depended on the biological continuity of each component between crops and fallows (see Table 1.4 and Figure 1.4a,b).

All statistical analyses were done using SAS software 6.14 (Hatcher and Stepanski, 1994). 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 *vs.* observed data (Pavé, 1994). Analyses of variance (Anova) were performed with proc GLM on ranks of data due to the small size of the population measured, and uncertainty about normality of distributions of data and residues (Potvin and Roff, 1993). SNK multiple-comparison test was used to segregate treatments according to the mean of rank values ($\alpha=0.05$).

1.3. RESULTS

1.3.1. General trends

C contents were very stable among tree species and other plant biomass components (Table 1.2a,b). N and P contents were highest in tree leaves, herbaceous layer and fine roots of crop vegetation.

Table 1.2 Carbon, nitrogen and phosphorus content of: a. Plant components of the four main woody species. Contents for other species were estimated as the mean of these values. b. Other above- and below-ground plant components of cropped and fallow fields.

a.

Species	C (g 100g ⁻¹ DM)			N (g 100g ⁻¹ DM)			P (g 100g ⁻¹ DM)		
	Trunk / stump	Twig	Leaf	Trunk / stump	Twig	Leaf	Trunk / stump	Twig	Leaf
<i>Combretum geitonophyllum</i>	38.8	35.8	35.8	0.45	0.29	1.48	0.04	0.04	0.09
<i>Combretum glutinosum</i>	37.6	38.5	39.7	0.16	0.32	1.18	0.03	0.02	0.05
<i>Piliostigma thoningii</i>	37.3	37.0	37.5	0.23	0.37	1.55	0.02	0.03	0.08
<i>Terminalia macroptera</i>	36.5	37.6	36.1	0.16	0.18	1.15	0.02	0.02	0.07

Derived from Kairé (1999)

b.

	Herb. layer	Litter	Fine root	Coarse root	Stump
C (g 100g ⁻¹ DM)					
Groundnut	37.5 ±0.4		34.1 ±0.5	38.0 ⁺	38.0 ⁺
Fallow	34.4 ±0.9	33.1 ±0.5	34.3 ±0.4	36.6 ±0.4	37.0 ±0.8 [‡]
N (g 100g ⁻¹ DM)					
Groundnut	1.93 ±0.02		1.66 ±0.03	0.35 ⁺	0.35 ⁺
Fallow	0.72 ±0.05	0.51 ±0.03	0.78 ±0.05	0.40 ±0.03	0.41 ±0.06 [‡]
P (g 100g ⁻¹ DM)					
Groundnut	0.11 ±0.00		0.07 ±0.01	0.02 ⁺	0.02 ⁺
Fallow	0.07 ±0.01	0.03 ±0.00	0.04 ±0.00	0.03 ±0.00	0.02 ±0.01 [‡]

±: standard error. Groundnut plots: n=6. Fallow plots: n=11.

+ : estimated as the mean of coarse root's values from FA1a, FA1b and FA1c.

‡: estimated as the content of coarse root measured in fallows aged one to four years; used for the calculation of C, N and P stock values in fallows aged one to four years only.

See data in Appendix 6.

Fine roots: diameter ranging 0-2 mm. Coarse roots: diameter above 2 mm (stump not included).

The plant biomass of the whole ecosystem averaged 49 tDM ha⁻¹ among the cropped and fallow plots investigated. This corresponded to 18 tC, 250 kgN and 21 kgP per hectare, of which more than 40 % and 50 % of N and P respectively were stored in woody AGB (Table 1.3, Figure 1.4a). Stumps were the second contributors to the storage of DM, C, N and P in the ecosystem. There was a more than three fold increase of DM storage in woody AGB between one-year old fallow plots (14 t ha⁻¹) and those older than 18 years (43 t ha⁻¹), half of it being stored in trunks in oldest fallows. C (from 5.1 to 15.9 t ha⁻¹), N (75 to 161 kg ha⁻¹) and P (7 to 21 kg ha⁻¹) amounts showed temporal patterns similar to DM during the fallow succession, though N storage occurred mainly in leaves. Stump biomass doubled meanwhile, reaching 15 t ha⁻¹ and storing 26 % of N and 17 % of P contained in the woody vegetation. Herbaceous biomass averaged 3.0 t ha⁻¹ (1.1 tC ha⁻¹) in crops and it increased to 6.0 t ha⁻¹ in youngest fallows but dropped to 1.6 t ha⁻¹ in the two oldest fallows. Organic and nutrient amounts in fine and coarse roots increased four (N) and six (P) folds between crops and oldest fallows, finally reaching 20 tDM, 7.2 tC, 88 kgN and 8.1 kgP per hectare. Fine roots represented 14 % of root biomass but more than a third of N and P storage in roots (not including stumps). Fine roots distribution between soil layers did not differ through the chronosequence; half of it was stored in the upper 10 cm. Shoot:root ratio averaged 0.22 in crops. It was higher in fallows aged less than 10 years than in older plots of the succession (0.62 *vs.* 0.56).

Table 1.3 Dry matter storage ($t\ ha^{-1}$) in plant components under a crop-fallow succession.

Plot	AGB ⁽¹⁾				Litter	Root				Stump	ABB ⁽²⁾		
	Woody		Herb.			Fine (per sampling depth in cm)							
	Trunk	Twig	Leaf	Total		0-10	10-20	20-30	30-40			Coarse	
GN01				0.13	2.37			0.19	0.15	0.11	0.07	5.2	
GN02				0.02	3.41			0.20	0.17	0.10	0.07	3.0	13.8
GN03				0.29	2.34			0.25	0.16	0.12	0.08	3.1	5.0
GN04				1.20	3.45			0.33	0.18	0.11	0.07	3.0	3.5
GN05				0.24	2.76			0.21	0.09	0.08	0.05	2.9	
GN06				0.03	3.42			0.29	0.18	0.10	0.07	3.0	
FA1a					6.51	1.84		0.78	0.28	0.20	0.14	5.4	3.5
FA1b					5.51	2.10		1.17	0.28	0.25	0.26	8.6	13.8
FA1c					4.99	1.53		0.81	0.16	0.22	0.19	3.4	5.0
FA1d													4.3
FA1e	2.2	1.3	0.8	4.3									16.9
FA1f	8.0	5.3	3.6	16.9									19.8
FA2a					6.01	0.57		0.72	0.27	0.30	0.20	5.9	11.7
FA2b	11.5	7.5	5.1	24.1									20.8
FA3a	5.9	3.2	1.4	10.5									8.0
FA3b	14.7	9.1	5.8	29.6									23.0
FA3c	12.4	8.2	4.5	25.1									19.8
FA4					9.45	2.77		0.90	0.28	0.21	0.16	4.7	4.7
FA6a	15.4	9.0	6.2	30.6									11.5
FA6b	15.8	9.0	4.4	29.2									15.6
FA7a					3.32	2.97		1.11	0.57	0.44	0.34	13.8	
FA7b	16.2	8.5	3.3	28.0									11.1
FA10a	19.8	11.4	6.7	37.8									11.8
FA10b	21.6	11.4	6.0	39.0									17.7
FA12					1.93	3.86		1.19					14.3
FA13a					0.96	1.19		1.82	1.19	0.74	0.68	19.6	
FA13b	21.5	10.5	3.9	35.9									12.5
FA15a	24.0	13.3	7.7	45.0									12.0
FA15b	22.3	11.8	6.2	40.4									18.6
FA17					2.15	2.65		1.32					15.8
FA18a					1.81	1.75		1.22	0.74	0.62	0.53	14.1	
FA18b	27.0	11.5	5.8	44.3									15.4
FA25	22.5	12.1	6.4	41.0									13.8
FA26					1.43	1.73		1.21	0.80	0.69	0.82	19.9	17.6

GN: groundnut crop. FA: fallow; the associated number stands for the age of fallow (in years).

⁽¹⁾ AGB: live above-ground biomass. Derived from Kairé (1999).

⁽²⁾ ABB: available biomass for burning. Derived from Kairé (1999).

Fine roots: diameter ranging 0-2 mm. Coarse roots: diameter above 2 mm (stump not included)

1.3.2. Adjustment of temporal dynamics of C, N & P in plant biomass to the logistic model during fallow

Best fits to the model were found for data of DM and C in woody and herbaceous AGB (Table 1.4, Figure 1.4a). A threshold was observed as from 10 years of fallow, whatever the variable and the component, except for stumps for which initial biomass was already substantial. However, different patterns were noticed before the threshold was reached, depending on variable and component. Models adjusted to data of AGB components showed no point of inflection, indicating maximum growth during the first years of fallow; this was not the case with coarse root DM and C, and fine root N and P storage (Figure 1.4b). Estimating herbaceous and fine root biomass as linear functions of respectively woody AGB, and woody and herbaceous AGB, led to little loss of explanatory power of the model, although it modified the aspect of the curves for N and P storage in fine roots.

Table 1.4 Estimates for parameters of a regression of $S = \{\text{amount of dry matter, carbon, nitrogen or phosphorus}\}$ on $t = \text{length of fallow}$, according to a logistic-like model: $S(t) = \frac{a.K}{1 + \frac{(K - S_0)}{S_0} \cdot e^{-r \cdot t}} + b$.

Unit	Component	Constraint(s)	a	K	So	r	b	R ²	F	p>F	n	p{Ho:intercept=0}	p{Ho:slope=1}
DM (t ha ⁻¹)	Woody layer	(1)	1	1150.3	1109.9	0.275	-1109.59	0.91	212.8	***	23	0.64	0.39
	- trunk	(1)(2)	1	580.7	557.0	0.211	-556.80	0.87	97.8	***	17	0.79	0.63
	- twig	(1)(2)	1	281.2	269.8	0.340	-269.69	0.71	37.2	***	17	0.24	0.18
	- leaf	(1)(2)	1	138.07	132.51	0.648	-132.44	0.27	5.6	*	17	***	***
	Herbac. layer	Low : (2)	1	1.60E-03	6.94	4.14E-05	0.00	0.90	75.3	***	10	0.41	0.35
		High : (3)	-0.14	1150.3	1109.9	0.275	159.33	0.89	67.2	***	10	0.43	0.36
	Fine root	Low : (1)	1	113.29	110.31	0.204	-109.74	0.89	121.1	***	17	0.63	0.39
		High : (4)	0.07	1150.3	1109.9	0.275	-75.20	0.88	110.3	***	17	0.25	0.17
	Coarse root	(1)	1	15.1	1.4	0.444	2.01	0.89	122.1	***	17	0.64	0.37
	Stump	(1)	1	15.54	7.77	0.211	-0.31	0.41	11.3	**	18	**	***
C (t ha ⁻¹)	Woody layer	(1)	1	416.3	401.2	0.278	-401.09	0.91	211.1	***	23	0.63	0.38
	- trunk	(1)(2)	1	255.8	246.9	0.212	-246.84	0.86	95.8	***	17	0.77	0.62
	- twig	(1)(2)	1	111.11	106.84	0.339	-106.80	0.72	38.1	***	17	0.24	0.18
	- leaf	(1)(2)	1	46.59	44.49	0.650	-44.46	0.28	5.9	*	17	***	***
	Herbac. layer	Low : (2)	1	0.00	2.69	4.31E-05	0.00	0.93	114.0	***	10	0.48	0.42
		High : (3)	-0.14	416.3	401.2	0.278	60.51	0.93	100.8	***	10	0.54	0.46
	Fine root	Low : (1)	1	24.73	23.70	0.198	-23.50	0.88	113.2	***	17	0.66	0.40
		High : (4)	0.06	416.3	401.2	0.278	-24.79	0.87	100.4	***	17	0.23	0.16
	Coarse root	(1)	1	5.10	0.25	0.548	1.04	0.88	107.3	***	17	0.69	0.38
	Stump	(1)	1	5.50	2.75	0.202	0.08	0.37	9.6	**	18	**	***
N (kg ha ⁻¹)	Woody layer	(1)	1	4086.1	3930.9	0.405	-3929.41	0.82	97.4	***	23	0.25	0.11
	- trunk	(1)(2)	1	1510.8	1457.4	0.229	-1457.06	0.72	38.5	***	17	0.31	0.21
	- twig	(1)(2)	1	777.5	745.9	0.383	-745.60	0.66	29.2	***	17	0.11	0.08
	- leaf	(1)(2)	1	1826.7	1755.5	0.708	-1754.61	0.22	4.3	0.05	17	***	***
	Herbac. layer	Low : (2)	1	1.12E-02	37.60	3.33E-05	0.00	0.86	47.7	***	10	0.31	0.27
		High : (3)	-0.19	4086	3931	0.405	798.91	0.78	27.9	***	10	0.20	0.17
	Fine root	Low : (2)(5)	1	17.2	0.1	1.036	9.63	0.87	59.2	***	11	0.46	0.38
		High : (4)	0.16	4086	3931	0.405	-637.50	0.78	32.7	***	11	0.18	0.15
	Coarse root	(1)	1	1254.5	1195.4	0.134	-1183.63	0.89	123.3	***	17	0.34	0.22
	Stump	(1)	1	66.1	33.0	0.272	-7.20	0.44	12.7	**	18	***	***
P (kg ha ⁻¹)	Woody layer	(1)	1	463.0	442.5	0.247	-442.33	0.91	212.3	***	23	0.72	0.60
	- trunk	(1)(2)	1	500.6	484.3	0.204	-484.19	0.86	91.1	***	17	0.84	0.67
	- twig	(1)(2)	1	83.02	80.14	0.365	-80.12	0.56	18.9	***	17	0.09	0.06
	- leaf	(1)(2)	1	33.70	32.20	0.978	-32.18	0.12	2.0	0.18	17	***	***
	Herbac. layer	Low : (2)	1	1.23	4.84	0.159	0.00	0.83	39.7	***	10	0.30	0.25
		High : (3)	-0.13	463.0	442.5	0.247	60.95	0.82	36.8	***	10	0.27	0.22
	Fine root	Low : (2)(5)	1	0.82	0.00	0.748	0.60	0.88	68.9	***	11	0.38	0.34
		High : (4)	0.05	463.0	442.5	0.247	-22.83	0.80	37.1	***	11	0.20	0.18
	Coarse root	(1)	1	359.77	350.53	0.052	-349.85	0.87	100.6	***	17	0.22	0.12
	Stump	(1)	1	5.89	2.94	0.229	-1.45	0.71	39.1	***	18	**	**

Constraints:

(1) sets $S(0)$ as the average value of S measured in crops.

(2) excludes crop data for model parameterisation.

(3) sets $S_{\text{herbaceous layer}}$ as a linear function of $S_{\text{woody layer}}$

(4) sets $S_{\text{fine root}}$ as a linear function of $S_{\text{herbaceous layer}}$ and $S_{\text{woody layer}}$

(5) sets $S(1)$ as the average value of S measured in one-year old fallows.

F test performed on R² and slope of linear regression of observed vs. predicted (t-test on the intercept).

p(:): * < 0.05; ** < 0.01; *** < 0.001.

Fine roots: diameter ranging 0-2 mm. Coarse roots: diameter above 2 mm (stump not included).

See data in Appendix 7.

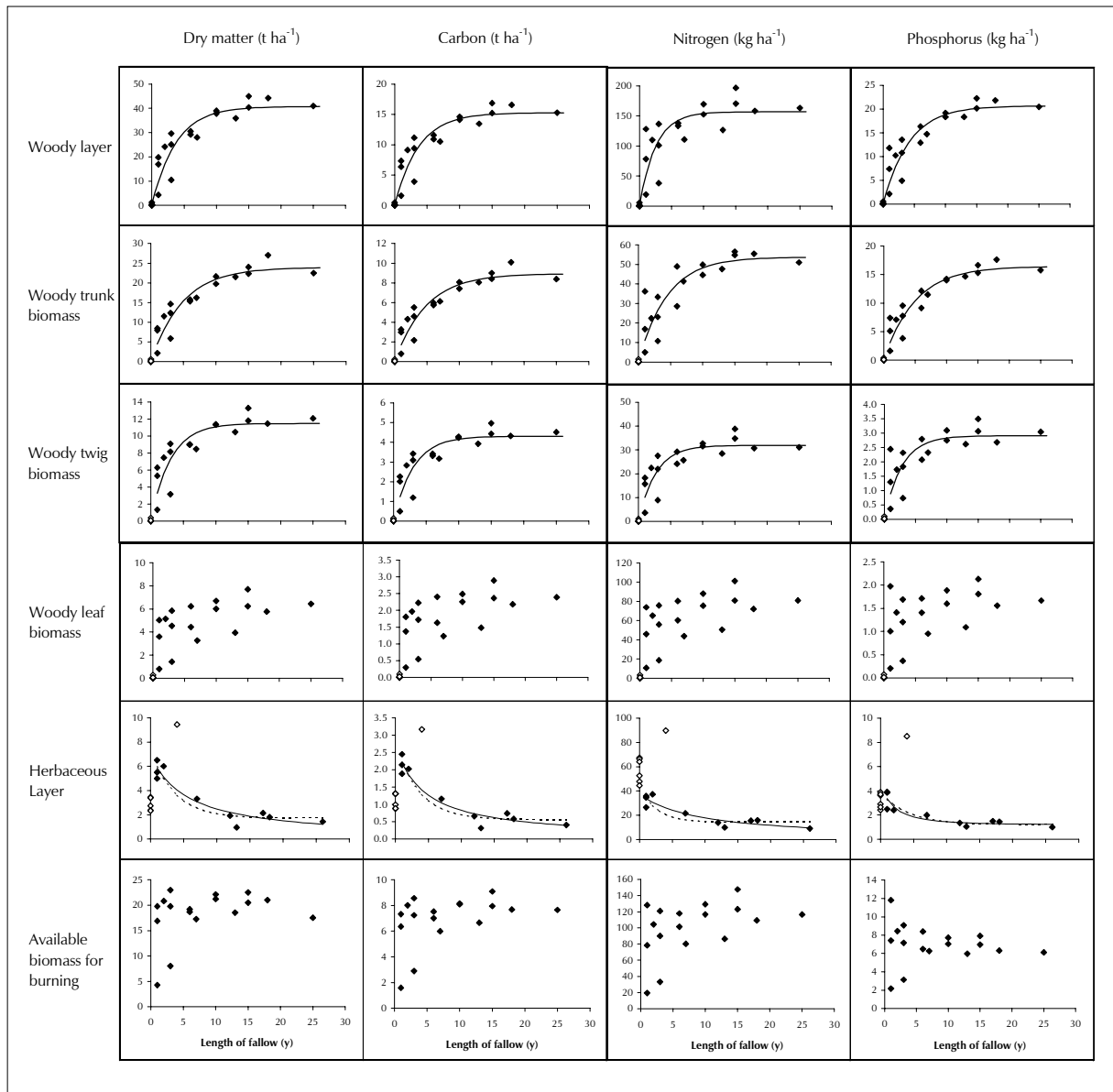


Figure 1.4 Dry matter, carbon, nitrogen and phosphorus storage in plant biomass during a crop-fallow succession, and fitting to a

modified, logistic-like model:
$$S(t) = \frac{a.K}{1 + \frac{(K - S_0)}{S_0} \cdot e^{-r \cdot t}} + b .$$

a. above-ground components.

Plain line: low-constraint model (see text and Table 1.4). Dotted line: high-constraint model. Plain dots: data used for model adjustment.

Fine roots: diameter ranging 0-2 mm. Coarse roots: diameter above 2 mm (stump not included).

See data in Appendix 7.

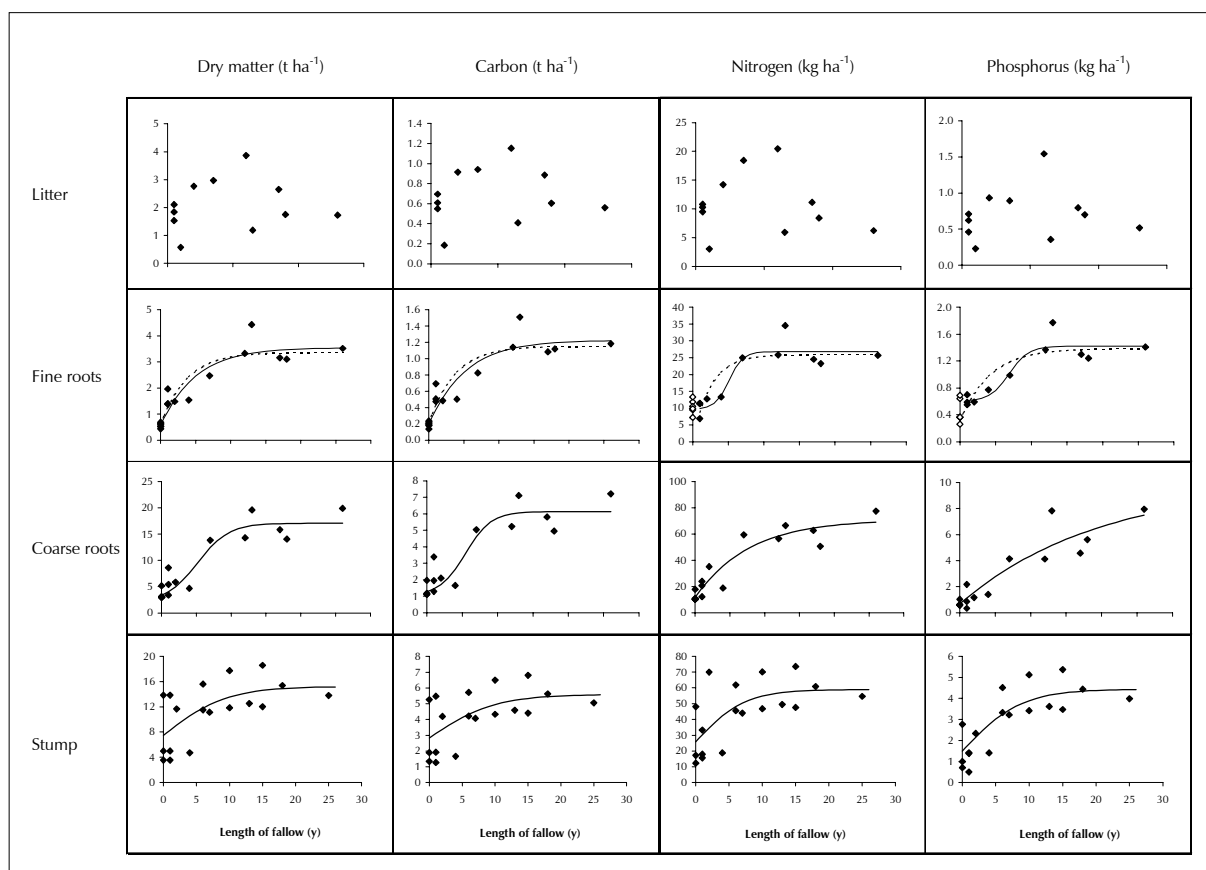


Figure 1.4 (continued) b. below-ground components

Plain line: low-constraint model (see text and Table 1.4). Dotted line: high-constraint model. Plain dots: data used for model adjustment.

All below-ground values calculated for the 0-40 cm layer.

See data in Appendix 7.

Fine roots: diameter ranging 0-2 mm. Coarse roots: diameter above 2 mm (stump not included)

1.3.3. Statistical analyses

Considering the quite stable value of the length of fallow beyond which no clear evolution of plant biomass and nutrient storage could be observed (see 3.2), data were clustered in three groups: groundnut fields (GN); young fallows (YF) aged less than 10 years; old fallows (OF) aged 10 years or more.

Table 1.5 Simplified budget and annual increase of dry matter, carbon, nitrogen and phosphorus in above- and below-ground plant biomass during a crop-fallow succession.

	Total storage			Annual variation (acc. to years of fallow)		
	Groundnut field	Young fallow	Old fallow	0-1 y	1-10 y.	10-25y.
DM (t ha ⁻¹)						
AG biomass	3.3	29.7	44.4	17.9	2.1	0.0
BG biomass	11.4	18.3	34.8	3.4	1.6	0.2
C (t ha ⁻¹)						
AG biomass	1.2	11.0	16.4	6.6	0.8	0.0
BG biomass	4.3	6.7	12.6	1.3	0.6	0.0
N (kg ha ⁻¹)						
AG biomass	59	151	186	59.2	9.0	-0.7
BG biomass	47	80	147	4.0	6.9	0.5
P (kg ha ⁻¹)						
AG biomass	3.3	15.0	22.1	7.8	1.0	0.0
BG biomass	2.6	4.6	11.6	0.3	0.7	0.1

Annual increases were estimated by using mean values calculated from the adjusted logistic-like model when available (see 1.3.2.), from a simple linear regression otherwise.

Table 1.6 Anova performed on dry matter, carbon, nitrogen and phosphorus amounts in plant biomass of cropped and fallow plots (young fallow: aged less than 10 years; old fallows: 10 years and more).

		Groundnut field		Young fallow		Old fallow		F
		Mean(±SE)	n	Mean(±SE)	n	Mean(±SE)	n	
DM storage (t ha⁻¹)								
AGB ⁽¹⁾	Woody, includ.	0.3 ±0.2 ^c	6	21.8 ±2.8 ^b	10	40.5 ±1.2 ^a	7	69.1 ***
	- trunk	nd		11.0 ±1.5 ^b	10	22.7 ±0.9 ^a	7	40.4 ***
	- twig	nd		6.7 ±0.9 ^b	10	11.7 ±0.3 ^a	7	40.4 ***
	- leaf	nd		4.03 ±0.57 ^b	10	6.11 ±0.43 ^a	7	10.1 **
	Herbaceous	2.96 ±0.22 ^b	6	5.97 ±0.83 ^a	6	1.65 ±0.21 ^c	5	29.6 ***
Litter		nd		1.96 ±0.36 ^a	6	2.24 ±0.47 ^a	5	0.0
Root	Fine 0-10 cm	0.24 ±0.02 ^c	6	0.92 ±0.08 ^b	6	1.35 ±0.12 ^a	5	56.5 ***
	10-20 cm	0.15 ±0.01 ^c	6	0.31 ±0.06 ^b	6	0.91 ±0.14 ^a	3	18.0 ***
	20-30cm	0.10 ±0.01 ^c	6	0.27 ±0.04 ^b	6	0.68 ±0.03 ^a	3	39.4 ***
	30-40 cm	0.07 ±0.00 ^c	6	0.22 ±0.03 ^b	6	0.67 ±0.08 ^a	3	45.6 ***
	0-40 cm	0.57 ±0.04 ^c	6	1.70 ±0.18 ^b	6	3.51 ±0.24 ^a	5	56.5 ***
	Coarse	3.4 ±0.4 ^c	6	7.0 ±1.5 ^b	6	16.7 ±1.3 ^a	5	35.2 ***
	Stump	7.5 ±3.2 ^a	3	9.6 ±1.6 ^a	8	14.6 ±1.0 ^a	7	3.5
C storage (t ha⁻¹)								
AGB ⁽¹⁾	Woody, includ.	0.1 ±0.2 ^c	6	8.2 ±1.1 ^b	10	15.2 ±0.47 ^a	7	69.1 ***
	- trunk	nd		4.15 ±0.57 ^b	10	8.49 ±0.32 ^a	7	40.4 ***
	- twig	nd		2.52 ±0.32 ^b	10	4.38 ±0.12 ^a	7	40.4 ***
	- leaf	nd		1.52 ±0.22 ^b	10	2.29 ±0.16 ^a	7	7.8 *
	Herbaceous	1.11 ±0.09 ^b	6	2.14 ±0.27 ^a	6	0.54 ±0.08 ^c	5	29.6 ***
Litter		nd		0.65 ±0.11 ^a	6	0.72 ±0.13 ^a	5	0.0
Root	Fine 0-10 cm	0.08 ±0.01 ^c	6	0.31 ±0.03 ^b	6	0.47 ±0.04 ^a	5	36.6 ***
	10-20 cm	0.05 ±0.00 ^c	6	0.10 ±0.02 ^b	6	0.31 ±0.05 ^a	3	18.0 ***
	20-30cm	0.04 ±0.00 ^c	6	0.09 ±0.01 ^b	6	0.24 ±0.01 ^a	3	39.4 ***
	30-40 cm	0.02 ±0.00 ^c	6	0.07 ±0.01 ^b	6	0.23 ±0.02 ^a	3	39.4 ***
	0-40 cm	0.19 ±0.01 ^c	6	0.58 ±0.06 ^b	6	1.21 ±0.08 ^a	5	56.5 ***
	Coarse	1.29 ±0.14 ^c	6	2.58 ±0.57 ^b	6	6.06 ±0.47 ^a	5	24.9 ***
	Stump	2.83 ±1.22 ^a	3	3.57 ±0.61 ^a	8	5.33 ±0.38 ^a	7	3.5
N storage (kg ha⁻¹)								
AGB ⁽¹⁾	Woody, includ.	1.5 ±0.9 ^c	6	99.4 ±13.2 ^b	10	162.5 ±8.0 ^a	7	42.7 ***
	- trunk	nd		26.7 ±4.4 ^b	10	51.4 ±1.7 ^a	7	27.6 ***
	- twig	nd		19.7 ±2.6 ^b	10	32.6 ±1.3 ^a	7	33.1 ***
	- leaf	nd		53.0 ±7.5 ^b	10	78.5 ±5.9 ^a	7	7.8 *
	Herbaceous	57.1 ±4.1 ^a	6	40.9 ±10.1 ^b	6	12.8 ±1.4 ^c	5	20.2 ***
Litter		nd		11.0 ±2.2 ^a	6	10.4 ±2.7 ^a	5	0.1
Root	Fine 0-10 cm	4.1 ±0.4 ^c	6	7.0 ±0.1 ^b	6	10.3 ±1.0 ^a	5	19.3 ***
	10-20 cm	2.6 ±0.2 ^b	6	2.5 ±0.7 ^b	6	6.9 ±1.2 ^a	3	6.4 *
	20-30cm	1.7 ±0.1 ^b	6	2.2 ±0.5 ^b	6	5.1 ±0.3 ^a	3	5.8 *
	30-40 cm	1.1 ±0.1 ^b	6	1.7 ±0.4 ^b	6	5.1 ±0.6 ^a	3	11.3 **
	0-40 cm	9.4 ±0.7 ^b	6	13.4 ±2.5 ^b	6	26.8 ±2.0 ^a	5	12.6 ***
	Coarse	11.7 ±1.2 ^c	6	28.3 ±6.9 ^b	6	62.8 ±4.6 ^a	5	29.7 ***
	Stump	25.9 ±11.2 ^b	3	38.4 ±7.3 ^{ab}	8	57.6 ±4.1 ^a	7	4.5 *
P storage (kg ha⁻¹)								
AGB ⁽¹⁾	Woody, includ.	0.1 ±0.1 ^c	6	10.5 ±1.4 ^b	10	20.1 ±0.6 ^a	7	69.1 ***
	- trunk	nd		7.5 ±1.0 ^b	10	15.5 ±0.5 ^a	7	40.4 ***
	- twig	nd		1.79 ±0.25 ^b	10	2.96 ±0.12 ^a	7	23.4 ***
	- leaf	nd		1.19 ±0.18 ^b	10	1.68 ±0.12 ^a	7	3.6
	Herbaceous	3.20 ±0.25 ^a	6	3.86 ±0.98 ^a	6	1.27 ±0.10 ^b	5	11.7 **
Litter		nd		0.64 ±0.11 ^a	6	0.78 ±0.21 ^a	5	0.0
Root	Fine 0-10 cm	0.18 ±0.03 ^c	6	0.37 ±0.03 ^b	6	0.55 ±0.05 ^a	5	43.4 ***
	10-20 cm	0.11 ±0.02 ^b	6	0.13 ±0.02 ^b	6	0.36 ±0.06 ^a	3	5.7 *
	20-30cm	0.07 ±0.01 ^c	6	0.11 ±0.01 ^b	6	0.27 ±0.01 ^a	3	15.1 ***
	30-40 cm	0.05 ±0.00 ^c	6	0.09 ±0.01 ^b	6	0.27 ±0.03 ^a	3	40.5 ***
	0-40 cm	0.41 ±0.06 ^c	6	0.70 ±0.07 ^d	6	1.42 ±0.09 ^a	5	25.6 ***
	Coarse	0.68 ±0.07 ^c	6	1.68 ±0.55 ^b	6	6.02 ±0.80 ^a	5	15.7 ***
	Stump	1.49 ±0.64 ^b	3	2.26 ±0.47 ^b	8	4.20 ±0.30 ^a	7	10.4 **

nd: not determined. Mean ± SE.

$p\{H_0: F_{obs} > F_{th}\}$: * < 0.05; ** < 0.01; *** < 0.001.

See data in Table 1.3 and Appendix 7.

Fine roots: diameter ranging 0-2 mm. Coarse roots: diameter above 2 mm (stump not included)

Mean amounts in plant biomass and net productivity (annual variation of the stocks) were summarised in Table 1.5. Fastest accumulation of elements generally occurred during the first year of fallow. This was not the case for below-ground N and P; fastest increases for these elements were achieved between one and 10 years of fallow. DM, C, N and P accumulation was 10 to 20 times slower beyond 10 years of fallow.

Anovas were performed on these three groups (Table 1.6). Significant increases of amounts of DM, C, N and P in woody AGB were found between GN and YF, and YF and OF. Herbaceous N and P values decreased through the succession, although highest biomass values were found in YF. Amounts in fine and coarse roots increased significantly along all steps of the succession, whatever the element. Although stump biomass strongly increased between YF and OF, differences were not statistically significant, except for P.

1.3.4. Post-fallow dynamics of above-ground plant biomass

Estimates presented below do not take into account possible translocation occurring during the dry season. Thus, N and P returns from AGB to the soil might be overestimated.

Herbaceous above-ground biomass. Estimates of potential returns of C, N and P from the herbaceous biomass to the soil would be 2.1 tC, 41 kgN and 3.9 kgP ha⁻¹ derived from a young fallow; 0.5 tC, 13 kgN and 1.3 kgP ha⁻¹ issued from an old fallow (Table 1.6). However, these are gross, upper estimates, as the returns of C and N to the soil at clearing heavily rely on fire occurrence.

Woody above-ground biomass (Figure 1.5). DM returns from a young fallow were estimated to be 8.4 t ha⁻¹ when setting combustion efficiency to 50 % of ABB, or 1.7 t ha⁻¹ under the 90 % hypothesis. Values computed for old fallows were 18.4 and 10.2 tDM ha⁻¹. This would mean an on-site recycling of 0.6-3.1/0.8-4.0 tC and 9-44/12-59 kgN ha⁻¹ depending on burning efficiency (90-50 %) and age of fallow (young/old). P returns to the soil would amount to 6.9 and 7.0 kg ha⁻¹, after clearing a young or an old fallow. Wood harvest occurring at clearing of an old fallow would lead to the following exportations: 50 % of DM and C, 27 % of N and 66 % of P contained in initial woody AGB.

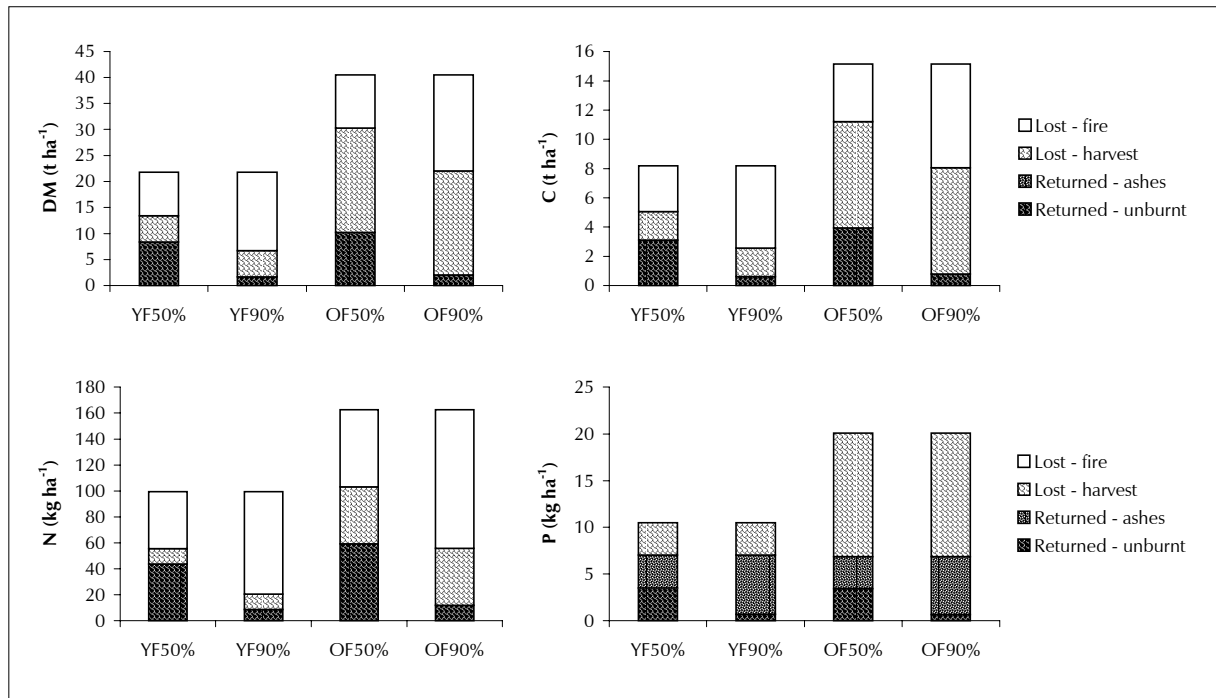


Figure 1.5 Fate of dry matter, carbon, nitrogen and phosphorus in above-ground woody biomass after clearing of a young (YF) and old (OF) fallow (young fallow: aged less than 10 years; old fallow: 10 years and more). Two scenarios are considered: 50 % and 90 % of available plant biomass for burning is burnt. Assumptions: ashes are DM-, C- and N-free; all P, except that exported for wood need, is returned to the soil both as ash or non-burnt biomass. See data in Appendix 8.

1.4. DISCUSSION

Plant biomass components show contrasted dynamics along the crop and fallow cycle. After crop abandonment woody and root biomasses increase at the expense of the herbaceous layer, while litter shows no clear pattern of evolution. These trends are consistent with observations made by Kotto-Same *et al.* (1997) under wetter conditions. However, even the highest amounts of carbon storage in plant biomass (29 t ha⁻¹) reported here are lower than the average values reviewed by Allen-Diaz *et al.* (1996) (118tC ha⁻¹) and Tiessen *et al.* (1998) (50tC ha⁻¹) for dry tropical forests and savannas. The potential for annual carbon sequestration in our study was similar to the work of Tiessen and his colleagues (5 t ha⁻¹) during the first year of fallow only. However, plant biomass and net storage productivity found in our study agreed better with those usually recorded in dry Miombo woodlands (AGB: 21-84 tDM ha⁻¹; BGB: 7-39 tDM ha⁻¹) (Desanker *et al.*, 1995). Meanwhile, amounts of nutrients in plant biomass were much lower than those reported by Singh and Singh (1991) in a dry Indian forest, higher than those reviewed by Lamotte and Bourlière (1983) (100-150 kgN and 19 kgP ha⁻¹), but roughly the same as an eight-year old fallow in a nearby area of Guinea (Sirois *et al.*, 1998).

Swift and Anderson (1994) have defined the concepts of productive biota – the community of plants and animals that provide peasants with valuable goods such as food or construction materials – and of resource biota – the body of “organisms which contribute positively to the productivity of the system”; this distinction will be the main backbone of the discussion.

1.4.1. Fallow as a productive ecosystem

Wood supplies 90% of the needs of rural population of the West African savannas for domestic energy and construction material (Bertrand, 1977; Breman and Kessler, 1995). However, estimates for wood standing stock values and productivity of fallows and woodlands of the sub-region are scarce and difficult to assess, because of uncontrolled fire, grazing, tree felling, and soil. For instance, Breman and Kessler (1995) report woody biomass values ranging 20-60 t ha⁻¹ in sub-Saharan Africa. Highest values of woody biomass found in our study were much lower than the mean estimates reported by Martinez-Yrizar (1995) in dry tropical forests (90 t ha⁻¹) and by Nye and Greenland (1960) in Ghanaian fallows and savannas (54 t ha⁻¹). This must be a consequence of pedohydric constraints due to shallow clay accumulation in soil and nutrient limited availability. Initial wood productivity averaged 2 tDM ha⁻¹ during the first ten years after crop abandonment; this is consistent with the estimates provided by Catinot (1994) (2-3 t ha⁻¹ y⁻¹) in managed savannas of the ecozone, though slightly lower than the figures reviewed by Alexandre and Kairé (2000) for West African secondary successions (2.5-4.7 t ha⁻¹ y⁻¹). In oldest fallows productivity dropped to 0.1 tDM ha⁻¹ y⁻¹, which is much less than FAO's findings (1989) for dry mature forests of the region (1.2 t ha⁻¹). Soil properties mentioned above may again be put forward for such a discrepancy. Tree felling by farmers, which cumulate value since crop abandonment was estimated to 2 tDM ha⁻¹ in local fallow fields (Kairé, 1999), has but little impact on woody productivity. To fulfil their need for domestic energy, peasants usually harvest dead wood rather than fell trees, because it saves labour. From Shackleton's work (1998) in south African savannas, local dead wood production might be estimated to 0.4 and 0.7 t ha⁻¹ in young and old fallows.

Pastoral usage of fallow usually conflicts with the need for woody products, as woody layer closure induces a fast decrease of herbaceous standing biomass in fallows older than ten years. Maximum grass biomass in youngest fallows averaged 6.5 t ha⁻¹, which compares fairly well with data of Nye and Greenland (1960) in savannas (1.5-7.6 t ha⁻¹), Fournier (1982) in Ivory Coast (3.5-9 t ha⁻¹) and Lamotte and Bourlière (1983) in a more humid savanna (7 t ha⁻¹). The herbaceous layer of fallow is a valuable source of forage for cattle, as it contributes to 75 % of the diet of local livestock (Delacharlerie, 1994). Recent results by Ickowicz (in press) suggest that fallows of intermediate age ensuring both forage quality and quantity have the best pastoral value among all vegetation facies of the uncropped plots of the study site.

1.4.2. Role of plant biomass in sustaining agro-ecosystem fertility

1.4.2.1. Cycling of nitrogen and phosphorus in plant biomass

The higher efficiency of plant communities of young fallows and pasture as compared to domestic plants for the restoration of substantial amounts of available nitrogen and phosphorus in soil, provided that

biological integrity has been maintained, has been demonstrated in several works and will not be discussed here (see Chapter 2). From an agro-ecological point of view, fallowing has been described as a process of organic matter and nutrient accumulation (Kowal and Kassam, 1978; Juo and Manu, 1996), something particularly obvious here during the year following crop abandonment (Table 1.5). Although removal of wood and grass during the fallow period -for purposes of energy and forage supply- remains locally negligible (Masse *et al.*, 1998), dramatic mineral losses from the ecosystem through felling or burning of woody and grass layers occur at clearing. Such practices imply the loss of 40-94 % of N contained in above-ground plant biomass (depending on combustion efficiency and fate of the herbaceous layer), and of 24-62 % of P (depending on the age of fallow). It may be hypothesised that N losses are of moderate consequences on yields of following crops, because groundnut is preferred to any other crop in the bush ring and it is a legume (although the N-fixation efficiency of local groundnut cultivars may be highly variable according to Pieri, 1989).

This is not the case with phosphorus, which is a non-renewable resource. Slash and burn practices can thus be justified only in a context where availability of labour power (human and motorised) is low (Nye and Greenland, 1960). Though often misstudied, the root component accounts for more than a third of total N and P storage in plant biomass. Considering P immobilisation in harvested groundnut biomass (2.8 kgP ha⁻¹), the clearing of a one-year old fallow could provide fairly enough P for three years of cropping, thanks to P returned to the soil both from cleared AGB and decaying root biomass (7.4 kgP ha⁻¹). As a matter of fact groundnut is never cropped longer than one year in High Casamance, indicating possible (1) pre-eminence of pest and weed problems, (2) asynchrony between nutrient release and plant needs throughout the first years of cropping, due to massive mineralization of plant biomass and SOM (Myers *et al.*, 1994), (3) fast conversion of P back to less available forms in soil. It must also be kept in mind that internal recycling (translocation) in tree was not taken into account in our calculations; it might lead to an overestimation of nutrient amounts stored in woody biomass at the end of the dry season (Breman and Kessler, 1995).

1.4.2.2. Carbon dynamics

Much evidence has been brought today about the non sustainability of strictly mineral fertilization in the tropics, and especially in West Africa (Pieri, 1989). Associated organic amendments are needed, since they maintain SOM levels and associated soil properties (Pieri, 1989; Tiessen *et al.*, 1994; Syers, 1997).

As mentioned above, only a small fraction of above-ground plant biomass returns to the soil at clearing and during the crop-fallow cycle. Therefore, soil organic inputs stem mainly from roots and, to a lesser extent, from litter. There is however a paucity of quantitative root dynamics studies in tropical savannas, especially in West Africa. In a drier site of Senegal, Chopart (1980) estimated groundnut fine root biomass to 0.3 t ha⁻¹, that is half of the values reported in this study. Mean fine root biomass of 20 Senegalese young grass fallows was estimated to 2 t ha⁻¹ by Charreau and Nicou (1971). In the Sudanian zone of Ivory Coast, César and Coulibaly (1993) also gave consistent values with our work (2.6 and 5.3 t ha⁻¹ of

fine roots in 10 and 15 years old fallows). General figures for woody root biomass in sub-Saharan Africa range 10-30 t ha⁻¹ (Breman and Kessler, 1995). The range of values of total root biomass found in this study compares well with estimates for less disturbed and more humid savannas (3.5 to 27 t ha⁻¹ according to Menaut and César, 1979) and for dry forests (23.4 t ha⁻¹ in Martinez-Yrizar, 1995).

Relative DM allocation to plant AGB as compared to BGB (shoot:root value) found in our study was 10 times less than that reviewed by Martinez-Yrizar (1995) for tropical dry forests, or that adopted by Delaney *et al.* (1997) for the estimate of BGB in dry forests of South America. Such a discrepancy might be explained by fire evenness. Advocating the fact that vegetation climax has not been reached after 25 years of fallow succession is not relevant: sacred, undisturbed woodlands found on the study site exhibit similar physiognomy to oldest fallows (unpublished observations).

Results of model adjustment (see 1.3.2.) indicate a time-lag of maximum growth rate between above- and below-ground components of the woody layer. Ecological implications of this time-lag are very important: it suggests that priority is given by woody plants to the development of autotrophic organs over rooting systems at the onset of the succession. Only later is more carbon allocated to below-ground biomass. This would result from competition for light according to Shukla and Ramakrishnan (1984), and for nutrients (mainly P) according to us. It demonstrates that the building of a strong rooting system in natural vegetation happens only in oldest fallows. This is of greatest importance to define sustainable rules of fallow management, because early fast plant biomass production -and soil improvement (Chapter 2)- recorded after crop abandonment must rely mostly on the resprouting capacity of woody plants.

In a more dynamic perspective, roots might account for 40 to 85 % of the net primary production of plant communities (Fogel, 1985). Root carbon originating from aerial parts returns to the soil through both exudation and decay of roots. Quantifying these inputs is a difficult task. Turn-over estimates under tropical dry climate range from 0.5 to 1.2 y⁻¹ (Menaut and César, 1979; Lamotte and Bourlière, 1983; Brown *et al.*, 1994). During the 1993-94 dry season, fine root biomass decreased by half in four local fallows (Manlay, 1994). Thus, using a turn-over value of 0.5 y⁻¹, C input from fine and coarse roots to the soil of young fallows would reach 1.6/3.6 tC ha⁻¹ y⁻¹. This is a rough evaluation of actual carbon flow, as it probably overestimates the turnover of coarse roots, but does not take into account root exudation.

1.5. CONCLUSION

From a strictly “productivist”, narrow point of view, appraisal of optimal length of fallow hangs more or less upon conflicting human needs and demographic context. In fallows disturbed mostly by fire, our results demonstrate the existence of an ecological threshold around 10 years after crop abandonment. A similar value was also recorded in the floristic and physiognomic studies of Stromgaard (1986) and Donfack *et al.* (1995) under equivalent climates; Brown and Lugo (1990) reviewed a higher value (15 years) in more humid successions. Beyond 10 years, the keeping of fallow for the production of valuable plant

biomass may be relevant under low population density only; from this study and findings of Shackleton (1998) indeed, old fallows would be more productive than the young ones only in term of dead wood production. Growing needs for both wood and forage would be met with 6-10 years old fallows at best. Nutrient budgets (N and P) indicate that such fallows might be of greatest efficiency to satisfy the needs of cropped plants during several years, although local practices of clearing lead to important losses of nutrients. However, the value of such an ecological threshold must rely largely on (1) the way local practices are applied at clearing, (2) the intensity of cropping, (3) the duration of human settlements. And much different patterns of vegetation dynamics are to be found in secondary successions, depending on how trees have to rely on resprouting capacity of stumps (low human pressure context) or on seedling strategies (high anthropisation scenario).

On the other hand, all these “nutrient” and “productivist” considerations are fairly restrictive. The well-known decline of yields in the overcrowded Groundnut Belt of Central Senegal, just 200 km far from the study site, and after several decades of mining agriculture, must remind that the short fallow-groundnut rotation is seldom sustainable (Pieri, 1989). Our study suggests that, when unavoidable, substitutes for long breaks of fallow must at least ensure strong root biomass settlement, soil energy replenishment, and subsequent modifications of functional ecological organisation enabling pest control. Alternative techniques to prolonged fallowing can be aimed at accelerating succession with improved fallows (Peltier, 1993; Harmand and Njiti, 1998) or inserting fallow ecological mechanisms of soil fertility conservation in continuous cultivation systems through the adoption of “dispersed tree” plantation in cropped fields or live-hedges systems, and stump-saving, no-till practices.