

Influence of trees on above-ground production dynamics of grasses in a humid savanna

Mordelet, Patrick & Menaut, Jean-Claude

Ecole Normale Supérieure, Laboratoire d'Ecologie, C.N.R.S. U.R.A.-258, 46 rue d'Ulm, 75230 Paris Cédex 05, France; Tel. +33 1 44323778; Fax +33 1 44323885; E-mail MORDELET@WOTAN.ENS.FR

Abstract. Above-ground grass biomass, necromass and tree litter were measured monthly over a vegetation cycle under tree clumps and in the open, in a humid savanna in Côte d'Ivoire. Grass production was calculated using several methods to better discriminate the contribution of the different grass compartments. Above-ground grass biomass is higher in the open than under canopies during the second part of the growing season, but there is no difference in grass necromass dynamics. Physical protection of grass necromass by tree litter against decaying under tree canopies was assumed to explain this discrepancy. Grass production, calculated as the sum of positive increments of biomass and necromass, equals $1073 \text{ g m}^{-2} \text{ yr}^{-1}$ in the open, against 74 % underneath trees. However, basal ground cover is only 50 % of that in the open. Comparison with other savanna studies as a whole does not show any significant effect of rainfall on the relationship between under-canopy and outside-canopy grass production. However, in arid conditions, grass production tends to increase under light-canopied trees (mostly *Acacia* legumes) which hardly affect grass photosynthesis, but add high quality litter to the soil surface.

Keywords: Canopy effect; Côte d'Ivoire; Lamto; Tree/grass relationship; West Africa.

Introduction

Savannas represent ca. 20 % of the world's terrestrial area and more than 50 % of the southern continents. They are characterized by a continuous grass layer coexisting with more or less densely scattered trees (Frost et al. 1986). Savanna structure and dynamics is considered to be mostly determined by soil moisture, soil nutrients, fire and herbivores which act on the interrelationships of trees and grasses (Skarpe 1992). Generally, both layers are considered to develop competitive interactions (Walter 1973; Walker & Noy-Meir 1982; Knoop & Walker 1985). However, by modifying resource availability to understorey grasses (Kessler & Breman 1991; Vetaas 1992), trees can produce either detrimental or beneficial effects on grass production. In East Africa, Belsky et al. (1989) and Weltzin &

Coughenour (1990) found a higher production under tree canopies. In contrast, in Southern Africa, Grunow & Bosch (1980) observed a lower understorey biomass suitable for grazing, and in West Africa, in an agricultural system, Kessler (1992) found lower sorghum grain yields under trees. The above-mentioned studies deal with isolated trees, generally legumes, whereas our study of a natural humid savanna in West Africa concerns the effect of non-leguminous tree clumps, isolated trees being uncommon in this savanna.

The aim of the study was to determine the relationship between tree clumps and grass biomass dynamics and production. A detailed analysis of the impact of tree cover on grass dynamics should enable a more accurate estimate of savanna grass production at site and landscape levels than formerly made by Menaut & César (1979). Such processes may be incorporated in the model of savanna functioning developed for Lamto by Gignoux (1994) to explore the effect of fire intensity and heterogeneity on tree community dynamics.

Study site

The study was conducted at the Tropical Ecology Station of Lamto, Côte d'Ivoire ($6^{\circ} 13' \text{ N}$, $5^{\circ} 02' \text{ W}$) at the forest-savanna boundary. Mean rainfall is 1200 mm/yr and varies considerably in seasonal distribution and annual total (data from Lamto Geophysical Station since 1962). Mean annual temperature is ca. 27°C with a very small seasonal variation ($\pm 1^{\circ} \text{C}$). Soils are tropical ferruginous soils with sandy texture. The work was located in the most widespread savanna type, the shrub facies, where trees are mostly gathered into plurispecific clumps (Menaut & César 1979). On the sample site, trees belong to three species only: *Crossopteryx febrifuga* (Afzel. ex G. Don) Benth., *Bridelia ferruginea* Benth. and *Cussonia barteri* Seeman. Both in the open and under tree clumps, the herbaceous layer is continuous and consists for more than 90 % of perennial tufted *Poaceae* (Menaut & César 1979). *Hyparrhenia diplandra* (Hack.) Stapf is the dominant grass on the sample site.

Annual bush fires destroy the grass layer and drastically limit tree recruitment (Menaut 1977) except under tree clumps where fire intensity decreases and seedling survival increases (Gignoux 1994). Such an effect is usually attributed to a change in grass fuel biomass and structure under tree clumps. There is no livestock and hardly any wild ungulates in Lamto.

Material and Methods

18 tree clumps were arbitrarily selected in such a way that isolated woody individuals, whatever their size, and other tree clumps do not affect control samples from open areas. These 18 tree clumps represent 50 % of the tree cover provided by clumps in the 3-ha plot where total woody cover was 19 %. Average number of trees was 4.25 (S.E. = 0.33) per clump, maximum height 9 m (S.E. = 1), projected crown area 85 m² (S.E. = 5) per clump and trunk area 0.39 m² (S.E. = 0.04) per clump.

The basal ground cover of grass tufts was measured 15 days after a bush fire, when the tuft bases were still conspicuous. Eight radial transects per tree clump were chosen at random on which vegetation was sampled on 2 m long segments under tree clumps and in the open (144 segments in each situation).

The above-ground phytomass dynamics of grasses were determined from the same clumps. As the canopy of each clump was not large enough to support more than ten plots without disturbing the neighbouring plots, six tree clumps per month were sampled from February 1989 to February 1990. All sample plots were chosen at random and marked in the field before the experiment was started, in order to avoid any disturbance during vegetation growth. The vegetation was harvested on two 1-m² plots under each tree clump and two in the open near each clump (12 m² each month for each situation). Under tree clumps, plots were 2 m inside the canopy edge, whereas in the open they were only 3 m away from the canopy edge due to occasional occurrence of neighbouring trees. Above-ground phytomass was clipped at ground level. Green biomass was sorted by species to compare the abundance values for the dominant species in both situations. Standing dead material was differentiated from green biomass and added to grass litter to give grass necromass. Tree litter was also collected. Samples were oven-dried and weighed.

The assessment of grass production is highly dependent on the method of calculation. Singh et al. (1975) showed that the choice of method can influence the conclusions. Summing production by species or species groups has not been selected due to the high variance in the data. For some species, variations in space can be greater than variations over time and can lead to an

overestimation of production (Singh et al. 1975), associated with large error terms (Singh & Yadava 1974). In order to compare grass production in open and canopy situations, several methods of calculations, chosen for their relevance to local field conditions, have been used (see Table 3, below). A small difference between both situations might well be concealed by methods of calculating net above-ground primary production. The maximum phytomass (method (a) in Table 3) or peak biomass (b) produces lower values than the actual grass production because all species do not reach their peak at the same time, and because decomposition occurs during the growing season. Summing positive increments of phytomass (c), biomass (d), necromass (e) or both biomass and necromass (f) also results in underestimated production values, as it does not account for the decomposition of the litter compartment (Singh et al. 1975), especially at the end of the vegetation cycle, when biomass production does not balance mortality (Abbadie 1983). The last method (g) gives theoretically the most accurate values (Fournier & Lamotte 1983): positive increment of biomass is always taken into account, while positive increment of necromass is taken into account when increment of biomass is positive and when the absolute value of the increment of biomass is smaller than the increment of necromass (in this later case both are added).

Biomass data were subjected to analysis of variance with the SAS package (Anon. 1990). These data were log or square-root transformed to achieve normality. Differences between the means were tested according to the Scheffe's test (Scheffe 1959).

Results

Ground cover under tree clumps was half of that in the open (Table 1). It resulted from the different physiognomic traits of the herbaceous layer: first, the number of tufts per unit area was greater in the open, especially for tufts wider than 10 cm; second, the average tuft width was greater in the open.

The above-ground biomass dynamics was significantly modified by tree canopies (Fig. 1a). In the open, grass biomass increased until it peaked in October, at the beginning of the flowering period, and then decreased until fire occurred in mid-January. Under tree clumps, grass biomass followed the same trend as in the open at the beginning of the cycle but was significantly lower than in the open from June onwards. Although not significant, the apparent November peak is coherent with field qualitative observations showing that plant greenness remained longer under tree clumps than in the open and that the maximum of flowering occurred one

Table 1. Basal ground cover and tuft characteristics under tree clumps and in the open. Differences between under-canopy and open situation are all significant (Mann Witney U-test, $p < 0.0001$). Ground cover is expressed as %, i.e. linear m of ground covered by vegetation per sampled ground linear m.

	Under tree clumps		In the open	
	mean	(S.E.)	mean	(S.E.)
Ground cover (%)	6.23	(0.45)	12.03	(0.60)
Tuft number per linear m	1.32	(0.07)	2.06	(0.08)
Tuft width (cm)	4.54	(0.30)	6.23	(0.33)
No. of tufts wider than 10 cm	0.18	(0.03)	0.43	(0.03)

month later (November) under tree clumps than it did in the open (October). Stem height was slightly lower under tree canopies in November (Table 2). The biomass contribution of the main species to the total biomass was similar in the open and beneath tree clumps (Fig. 2). Nevertheless the specific composition was different in both situations, but the strict sun-loving and shade-loving species which contribute little to the total biomass were not separated (Menaut & César 1979). Under tree clumps, above-ground net production was between 51 and 90 % of that in the open, depending on the calculation method (Table 3).

Grass necromass showed no significant difference between open and canopy situations (Fig. 1b). Grass necromass was nearly completely burnt in mid-January and increased steadily by approximately 50 g/m² each month. In the open, woody litter remained very low all year (Fig. 1c). Beneath tree clumps, tree litter was also burnt by bush fires, with the remaining leaves falling during the few days after the fire. Two periods can be distinguished: from February to July-August, when tree litter decreases due to decomposition in the absence of further input; from August to January, when tree litter accumulates because of leaf fall, and in spite of decomposition.

Table 2. Number of stems per m² and mean height (cm) with associated standard error (S.E.) for *Hyparrhenia*, measured on 12 m × 1 m plots, in November and December 1989 and January 1990, in the open and under tree clumps. Differences between open and canopy situations for stem height are significant only in November (Mann Witney U-test).

Month	Situation	Number	Mean height	S.E.
November	Canopy	27	154	3.5
	Open	46	168	2.7
December	Canopy	24	146	4.1
	Open	56	140	2.4
January	Canopy	12	105	3.6
	Open	25	105	2.7

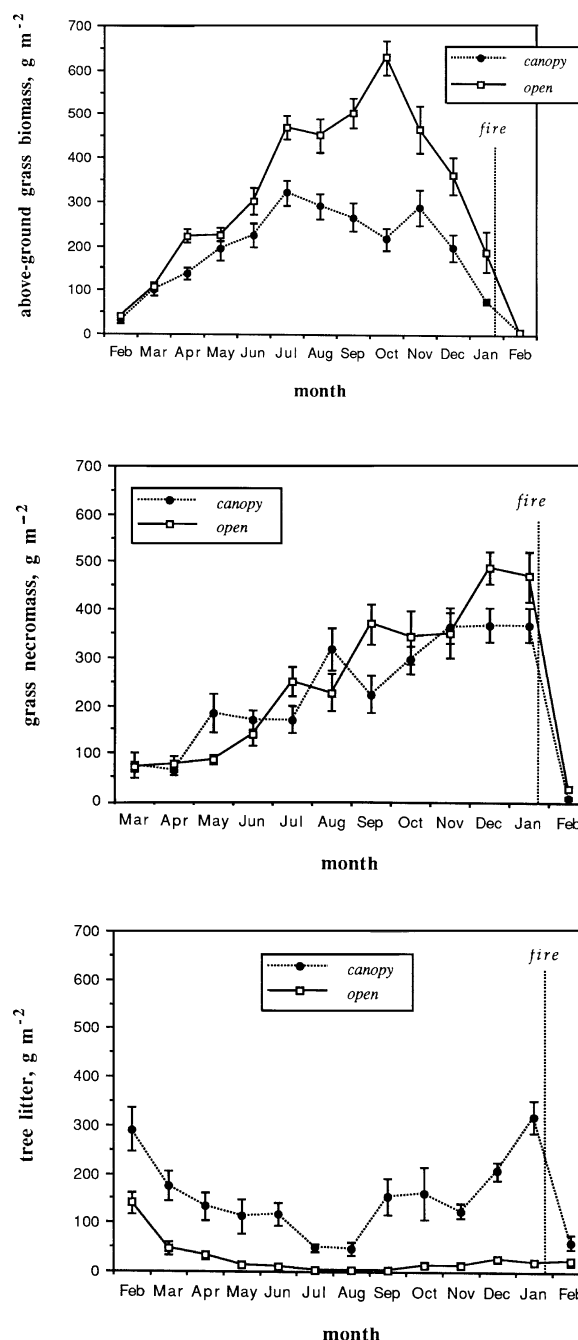


Fig. 1. Above-ground grass biomass dynamics (a), above-ground grass necromass dynamics (b) and tree litter dynamics (c) under tree clumps and in the open.

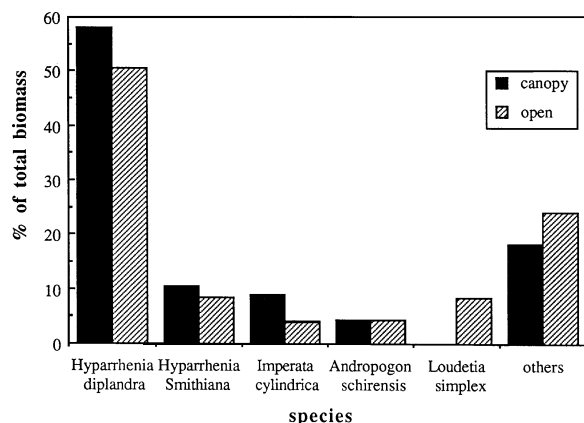


Fig. 2. Mean annual contribution of the main species to the total biomass under tree clumps and in the open.

Discussion

Under tree canopies, the herbaceous cover was sparser than in the open, due to a lower basal ground cover, with fewer and smaller tufts, and shorter stems. Two main hypotheses can be proposed to explain the difference between canopy and open conditions, both referring to the modification of environmental conditions under the canopy:

- Firstly, beneath tree clumps, soil water content dynamics is slightly lower during the growing season (Mordelet et al. 1993). However, from July to peak phytomass, soil water content remains above the water holding capacity, and water should be available in both situations. Accordingly, it should not account for much of the lower biomass under tree clumps.

- Secondly, evidence in a previous study indicated that shading by tree clumps in Lamto savanna can potentially limit grass photosynthesis (Mordelet 1993). Over a day, the assimilation rate can be five to six times lower for continuously shaded leaves under canopies than it is for leaves in open conditions in full sunshine. The detrimental effect of shading on primary production is partly balanced by sunflecks through the canopy but could nevertheless play a role.

Given that above-ground biomass was lower under tree canopies, necromass was expected to be lower under canopies. Greater potential microbial activity under tree clumps (Mordelet et al. 1993) should have increased the difference by increasing decomposition rates under canopies. However, there was no significant difference in herbaceous necromass. One hypothesis refers to the protection of grass litter by tree leaf litter. After fire, the remaining tree leaves fall on the bare ground. Tree litter is then directly available to termites which constitute the major agent of litter removal. Termites prefer tree litter to grass material (Lepage et al. 1993). In addition, tree leaf litter on the ground prevents grass litter from being in contact with the soil, thus reducing its decomposition rate. Outside canopy clumps, termites will consume grass litter in the absence of tree leaf litter. Thus dead grass material can accumulate in the presence of tree litter, i.e. under canopies.

In Lamto, in the open, Menaut & César (1979) calculated the total above-ground productivity of the herbs for *Andropogonae* savanna (summation of positive increments of biomass and necromass) as ranging from 12.8 t ha⁻¹ yr⁻¹ (open shrub savanna) to 16.1 (dense shrub savanna). For the same facies, the herb layer production varied, according to the calculation methods, from 7.0 to 13.9 t ha⁻¹ yr⁻¹ (César 1971) and from 9.4 to 12.8 t ha⁻¹ yr⁻¹ (Abbadie 1983). Our results are in good agreement with these previous studies but the

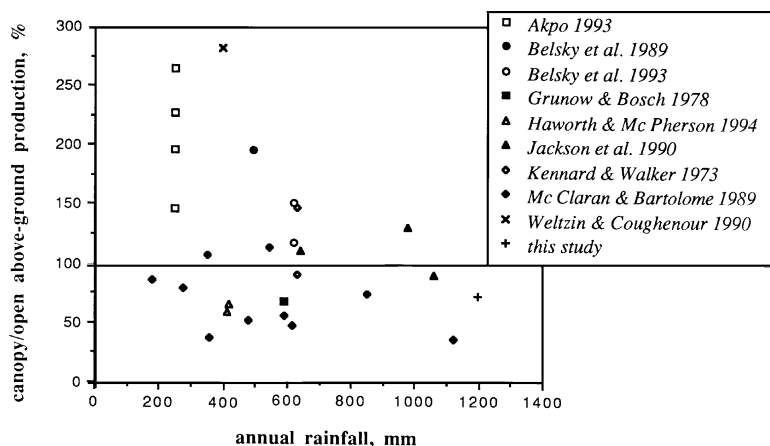


Fig. 3. Influence of trees on above-ground grass production, calculated as production beneath trees / production in the open (%), along a rainfall gradient.

Table 3. Grass production ($\text{g m}^{-2} \text{yr}^{-1}$) under tree clumps and in the open situation assessed by different calculation methods, and percentage of the production under tree clumps in relation to that in the open (%).

	Under tree clumps	In the open	%
a. Maximum of phytomass	(Nov.) 655	(Oct.) 977	67
b. Maximum of biomass	(Jul.) 322	(Oct.) 632	51
c. Sum of the positive increments of phytomass	771	1046	74
d. Sum of the positive increments of biomass - S1	394	648	61
e. Sum of the positive increments of necromass - S2	486	541	90
f. S1 + S2	880	1189	74
g. Sum of increments of biomass and necromass*	794	1073	74

* See text for explanation

comparison shows that in spite of a considerable amount of field work, the assessment of primary production is not accurate.

All calculation methods show lower grass production under canopies, varying from 51 to 90 % of the production in the open situation. According to the above hypothesis of a slower necromass decay under tree clumps, methods of calculation incorporating grass necromass should be considered with care, as production in open areas would probably be underestimated to a greater extent than under canopies.

Lower grass production values under canopies were also recorded in South African savannas (Grunow & Bosch 1978), but in East African savannas some authors found a higher grass production under isolated trees (Belsky et al. 1989; Weltzin & Coughenour 1990). Results of different studies along a rainfall gradient, in savanna formations *sensu lato*, show that the enhancement or depression of grass production by tree canopies is not related to rainfall (Fig. 3). However other processes could hide this effect:

1. Differences in calculation methods (which were not fully described in all quoted papers).
2. The effect of tree cover density and leaf area index of trees. Compared with the open situation, the highest grass production was recorded under acacia and baobab trees (Fig. 3, Belsky et al. 1989; Weltzin & Coughenour 1990), which are known to have light foliage and consequently should have a low light interception and only induce a slight limitation to photosynthesis. The importance of the density of tree canopy cover was also emphasized by Kennard & Walker (1973). They measured higher biomass of *Panicum maximum* under open canopies but lower under closed canopies as compared to open areas.
3. Soil enrichment by nitrogen fixing species, like acacias which results in an increase in yield (Dancette & Poulain 1969). The greatest enhancement of grass production is found under leguminous trees (Fig. 3, Belsky et al. 1989; Weltzin & Coughenour 1990).

The production under canopies relative to that in the open (ca. 70 %) differs clearly from the percentage of canopy/open basal ground cover (ca. 50 %). This implies that the production rate per unit of ground cover is higher under tree clumps than in the open. Apart from the possible bias induced by grass necromass dynamics, two environmental constraints suggest that the difference could result from differences in the allocation pattern of assimilates. It is predicted that the more a resource limits production, the more plants will allocate energy to acquiring this resource (Tilman 1990). First, organic carbon and total nitrogen content as well as potential microbial activity are higher under tree clumps (Mordelet et al. 1993). Consequently, nutrient uptake should be easier under tree clumps than in the open. Second, light interception by tree canopies should increase the allocation to the leaves in order to compensate for light deficiency. Thus, there should be higher shoot/root ratios under tree clumps. A higher shoot/root ratio under tree canopies was indeed reported in oak savannas (Jackson et al. 1990) and in East Africa (Belsky et al. 1989). Light interception by tree canopies is considered to be the most important factor responsible for the depletion of grass layer biomass and production under tree clumps, despite soil enrichment by tree litter. This reduces grass fuel and could result in fire heterogeneity which is supposed to play a major role in the dynamics of the woody community (Menaut et al. 1990; Skarpe 1991).

Acknowledgements. We express our gratitude to the National University of Côte d'Ivoire and to R. Vuattoux, Director of the Lamto Research Station for the facilities obtained. We also address our warm thanks to A. Konan N'Dri, F. Kouamé, E. Kouassi, G. Kouassi, M. Loukou, P. Sawadogo for their efficient technical assistance. We thank J. Gignoux for statistical advice and C. Skarpe for comments on the initial manuscript. The study was supported by grants from the CNRS (SALT-IGBP/GCTE Core Research Project).

References

- Anon. 1990. *SAS/STAT user's guide*. Cary, NC.
- Abbadie, L. 1983. Contribution à l'étude de la production primaire et du cycle de l'azote dans les savanes de Lamto (Côte d'Ivoire). Thesis. *Trav. Cherch. Lamto* 1: 1-135.
- Akpo, L.E. 1993. *Influence du couvert ligneux sur la structure et le fonctionnement de la strate herbacée en milieu sahélien*. Ed. ORSTOM, Paris.
- Belsky, A. J., Amundson, R. G., Duxbury, J. M., Rika, S. J., Ali, A. R. & Mwonga, S. M. 1989. The effects of trees on their physical, chemical, and biological environment in a semi-arid savanna in Kenya. *J. Appl. Ecol.* 26: 1005-1024.
- Belsky, A.J., Mwonga, S.M., Amundson, R.G., Duxbury, J.M. & Ali, A.R. 1993. Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. *J. Appl. Ecol.* 30: 143-155.
- César, J. 1971. *Etude quantitative de la strate herbacée de la savane de Lamto (moyenne Côte d'Ivoire)*. Thèse de 3ème cycle, Université de Paris.
- Dancette, C. & Poulain, J.F. 1969. Influence of *Acacia albida* on pedoclimatic factors and crop yields. *Afr. Soils* 14: 143-184.
- Fournier, A. & Lamotte, M. 1983. Estimation de la production primaire des milieux herbacés tropicaux. *Ann. Univ. Abidjan série E* 16: 7-38.
- Frost, P., Medina, E., Menaut, J.-C., Solbrig, O., Swift, M. & Walker, B. 1986. *Responses of savannas to stress and disturbance*. Biology International (I.U.B.S.), NTIS 10, Paris.
- Gignoux, J. 1994. *Modélisation de la coexistence herbes/arbres en savane*. Thèse de Doctorat de l'Institut National Agronomique Paris-Grignon.
- Grunow, J.O. & Bosch, O.J.H. 1978. Aboveground annual dry matter dynamics of the grass layer in a tree savanna ecosystem. *Proc. 1st Int. Rangeland Congress*, pp. 229-233. Range Management, Denver, CO.
- Grunow, J.O., Groeneveld, H.T. & Du Toit, S.H.C. 1980. Above-ground dry matter dynamics of the grass layer of a South African tree savanna. *J. Ecol.* 68: 877-889.
- Haworth, K. & Mc Pherson, G.R. 1994. Effects of *Quercus emoryi* on herbaceous vegetation in a semi-arid savanna. *Vegetatio* 112: 153-159.
- Jackson, L.E., Strauss, R.B., Firestone, M.K. & Bartolome, J.W. 1990. Influence of tree canopies on grasslands productivity and nitrogen dynamics in deciduous oak savanna. *Agron. Ecosyst. Environ.* 32: 89-105.
- Kennard, D.G. & Walker, B.H. 1973. Relationships between tree canopy cover and *Panicum maximum* in the vicinity of Fort Victoria. *Rhod. J. Agr. Res.* 11: 145-153.
- Kessler, J.J. 1992. The influence of karité (*Vitellaria paradoxa*) and néré (*Parkia biglobosa*) trees on sorghum production in Burkina Faso. *Agrofor. Syst.* 17: 97-118.
- Kessler, J.J. & Breman, H. 1991. The potential of agroforestry to increase primary production in the Sahelian and Sudanian zones of West Africa. *Agrofor. Syst.* 13: 41-62.
- Knoop, W.T. & Walker, B.H. 1985. Interactions of woody and herbaceous vegetation in a southern african savanna. *J. Ecol.* 73: 235-253.
- Lepage, M., Abbadie, L. & Mariotti, A. 1993. Food habits of sympatric termite species (*Isoptera, Macrotermitinae*) as determined by stable carbon isotope analysis in a Guinean savanna (Lamto, Côte d'Ivoire). *J. Trop. Ecol.* 9: 303-311.
- Mc Claran, M.P. & Bartolome, J.W. 1989. Effect of *Quercus douglasii* (Fagaceae) on herbaceous understory along a rainfall gradient. *Madroño* 36: 141-153.
- Menaut, J.-C. 1977. Evolution of plots protected from fire since 13 years in a Guinea savanna of Ivory Coast. *Actas del IV symposium internacional de ecologia tropical, Panama* 2: 541-558.
- Menaut, J.-C. & César, J. 1979. Structure and primary productivity of Lamto savannas, Ivory Coast. *Ecology* 60: 1197-1210.
- Menaut, J.-C., Gignoux, J., Prado, C. & Clobert, J. 1990. Tree community dynamics in a humid savanna of the Côte d'Ivoire: modelling the effects of fire and competition with grass and neighbours. *J. Biogeogr.* 17: 471-481.
- Mordelet, P. 1993. Influence of tree shading on carbon assimilation of grass leaves in Lamto savanna, Côte d'Ivoire. *Acta Oecol.* 14: 119-127.
- Mordelet, P., Abbadie, L. & Menaut, J.-C. 1993. Effects of tree clumps on soil characteristics in a humid savanna of West Africa (Lamto, Côte d'Ivoire). *Plant Soil* 153: 103-111.
- Scheffe, H. 1959. *The analysis of variance*. John Wiley & Sons, New York, NY.
- Singh, J.S. & Yadava, P.S. 1974. Seasonal variations in composition, plant biomass and net primary productivity of a tropical grassland at Kurukshetra, India. *Ecol. Monogr.* 44: 351-376.
- Singh, J.S., Lauenroth, W.K. & Steinhorst, R.K. 1975. Review and assessment of various techniques for estimating net aerial primary production in grassland from harvest data. *Bot. Rev.* 41: 181-232.
- Skarpe, C. 1991. Spatial patterns and dynamics of woody vegetation in an arid savanna. *J. Veg. Sci.* 2: 565-572.
- Skarpe, C. 1992. Dynamics of savanna ecosystems. *J. Veg. Sci.* 3: 293-300.
- Tilman, D. 1990. Constraint and tradeoff: toward a predictive theory of competition and succession. *Oikos* 58: 3-15.
- Vetaas, O.R. 1992. Micro-site effects of trees and shrubs in a dry savanna. *J. Veg. Sci.* 3: 337-344.
- Walker, B.H. & Noy-Meir, I. 1982. *Aspects of stability and resilience of savanna ecosystems*. In: Walker, B.H. & Huntley, B.J. (eds.) *Ecology of Tropical Savannas*, pp. 556-590. Springer-Verlag, Berlin.
- Walter, H. 1973. *Vegetation of the earth in relation to climate and the ecophysiological conditions*. Springer-Verlag, Berlin.
- Weltzin, J.F. & Coughenour, M.B. 1990. Savanna tree influence on understory vegetation and soil nutrients in north-western Kenya. *J. Veg. Sci.* 1: 325-334.

Received 8 August 1994;

Revision received 15 November 1994;

Accepted 23 November 1994.