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STRUCTURE AND PRIMARY PRODUCTIVITY OF LAMTO SAVANNAS, IVORY COAST[1]

J. C. MENAUT AND J. CESAR
Laboratoire de Zoologie (LA CNRS numéro 258), Ecole Normale Supérieure, 46 rue d'Ulm, 75005 Paris, France

Abstract. Lamto savannas (Ivory Coast) are characterized by the heterogeneity of their structure and by their dynamic evolution towards forest. Life-forms and phenological cycles of herbs, shrubs, and trees reflect the constraining factors of the environment. Biomass and productivity are largely dependent on soil and climate. The specific cycles of above- and belowground biomass allow an estimate of the primary productivity. Production of shrubs and trees, obtained from size-biomass correlations and growth measures, is compared with herb production to give an insight into the ecological balance of the savanna communities.

Key words: *above- and belowground biomass; Andropogoneae; Ivory Cast; life-forms;* Loudetia simplex; *phenological cycle; primary productivity; savanna; stability; structure.*

INTRODUCTION

The Lamto Reserve (5°02′W, 6°13′N; 200 km north of Abidjan, Ivory Coast) lies in the Guinea bioclimatic zone (precipitation ≈1300 mm/yr) girdling the west African rainforest (Lecordier 1974). The landscape is a forest-savanna mosaic. Savannas are intersected by fringing forests along the intermittent rivers and by remnants of the semideciduous forest situated on the richest plateau soils (Devineau 1975). Herbaceous communities occur between these two types of forest; trees and shrubs generally occur at low densities, the palm tree *Borassus aethiopum* being the tallest and the most characteristic. [Species nomenclature is from Hutchinson and Dalziel (1972).]

Adjanohoun (1964) classified these savannas in the *Brachiaria brachylopha* association, *Loudetia simplex* subassociation. The flora and vegetation of the Lamto savannas are very heterogeneous. The flora contains ≈400 savanna species (pyrophytes) and a number of woody species originating from the forest or from secondary thickets. The herbaceous cover mainly consists of grasses (75–90% of the total biomass); legumes are unevenly distributed, scarce, and often absent. Among the woody species, ≈30 are fire tolerant, come from the Sudan flora, and are acclimatized to humid conditions; the others come from the forest and occur in the savanna due to local favorable conditions. The floristic originality of Lamto savannas lies in their position at the boundary of the semideciduous, dense, humid forest. Maintained by fire in a forest area, they have an impoverished savanna flora which is liable to be invaded by forest species at any disruption of the present balance (Menaut 1977*b*).

DESCRIPTION OF THE VEGETATION

Main savanna facies

Most of the Lamto savannas lie on a granitic substratum that produces tropical ferruginous soils. These soils are more or less well drained or are hydromorphic according to their topographic position. The present study is limited to the analysis of a schematic catena on which the main savanna facies are represented (Fig. 1).

The pseudogley soils of the lower part of the slope are covered by a *Loudetia simplex* grass savanna. Trees and shrubs are rare, occur mostly on termite mounds, and, with the exception of the palms, they rarely grow above the grass layer. The most humid facies appear at the bottom of the slope which bears either a fringing forest or a swamp with sedges. On well-drained soils, Andropogoneae (*Andropogon schirensis, Hyparrhenia* spp., *Imperata cylindrica*) predominate in various densities in relation to the tree cover (Fig. 2). More than 90% of the woody communities are composed of four species: *Bridelia ferruginea, Crossopteryx febrifuga, Cussonia barteri,* and *Piliostigma thonningii.* Their density is extremely variable but, most often, an open shrubland (woody cover ≈5%) progressively changes to dense woodland as the plateau and better soil are reached. In the dense areas, the vegetation becomes a mosaic of open and closed facies. The open facies occur where soil concretions are abundant; in closed facies, shade-tolerant grass and forb species replace *Andropogon* spp. and *Hyparrhenia* spp. A fringe of vegetation characterized by *Cochlospermum planchoni* often occurs between *Loudetia* grass savannas and Andropogoneae shrublands, indicating the highest position of the water table during the wet season.

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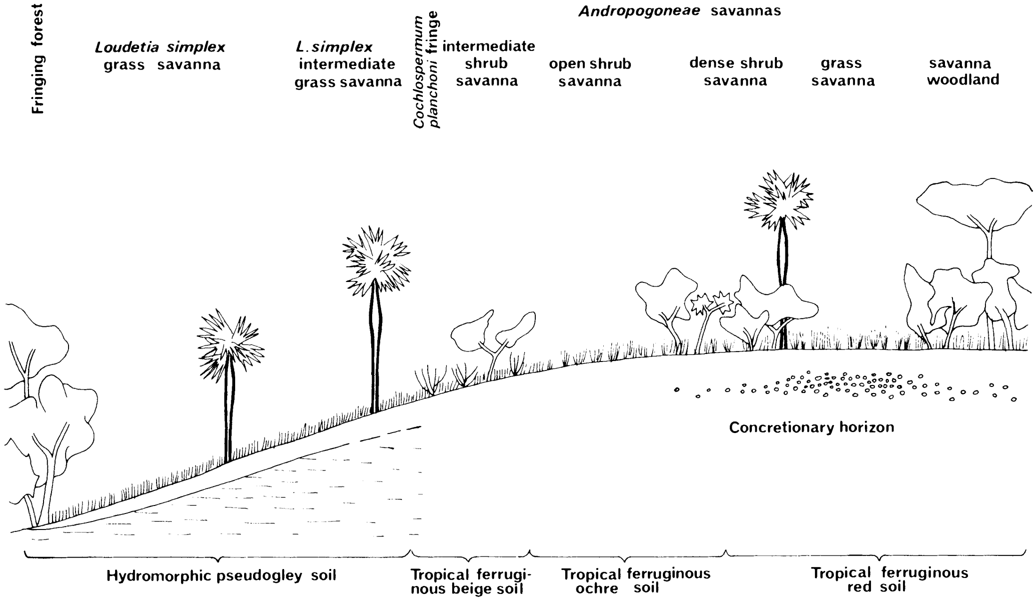


FIG. 1. Distribution of the main savanna facies on a schematic catena. In the field, the facies always occur in the present order but one or more may be absent on a catena.

Structure of the vegetation

Three broad strata have been described from statistical analysis of the height of plant species (César and Menaut 1974): a grass stratum with some low woody plants (0–2 m), a shrub stratum (2–8 m), and a tree stratum (>8 m). Generally, the tree stratum consists only of isolated palms. In the dense shrub and tree facies, the upper stratum is rich in mesophanerophytes such as *Erythrophleum guineense* or *Terminalia glaucescens*. In these conditions, shrubs such as *Crossopteryx febrifuga* or *Ficus capensis* are able to grow to their full height and connect the two woody strata that still remain rather distinct. A small proportion of individuals emerges from the dense shrub layer. This stratification is very clear on diagrams of height classes made for each of the main facies (Menaut 1971).

Ninety percent of the herb stratum is composed of grasses, the spread of which is nearly always continuous. The only exception is in the most closed formations where the herbaceous layer is sometimes discontinuous and may be invaded by forb species (Leguminosae, Rubiaceae). The tufts of most grasses result in a mosaic of soil and vegetation with bare ground between grass clumps. The basal cover of the grasses reaches ≈20% and varies little through the year. However, the mean size of tussocks depends on the environment. Tussocks are generally smaller and more diffuse in *Loudetia* savannas than in Andropogoneae savannas, but they become huge in marshy savannas. Fire maintains the tussocks and increases their cover by favoring tillering (César 1975). Within the grass layer are shoots of woody species, including some which appear as annual suckers from rootstocks (e.g, *Annona senegalensis*, *Bridelia ferruginea*, *Ficus capensis*, and particularly *Piliostigma thonningii*).

The density of woody plants >2 m varies from almost zero to 1500 stems per hectare, with a mean density of 250 per hectare. Shrubs may grow all over the savanna and their number increases with substrate qualities, but they are mostly distributed in patches and the mean cover is rather low (15–20%). Trees are generally isolated and dominate a shrub cluster. This patchy distribution appears to be controlled by edaphic factors and competition between grasses and tree seedlings, rather than fire.

Palms are much more regularly distributed in Lamto savannas and their size seems more related to soil qualities than to the density of trees. They withstand wet soil conditions or even flooding and are the only tree species in the *Loudetia* savannas. In marshy sites, they occur on termite mounds as does another palm, *Phoenix reclinata*. The distribution of *Borassus aethiopum* roots in the soil is rather homogeneous and suggests that intraspecific competition may be a major factor controlling the distribution of these palms (J. César, *personal observation*).

A comparison of the distribution of woody plants and the composition of the herb layer shows how shrubs and trees influence the herbaceous stratum. This mostly results from variations in the amount of shade and litter. The transition from an open grassland of species such as *Andropogon* and *Hyparrhenia* to a dense, woody vegetation with herbs such as *Imper-*

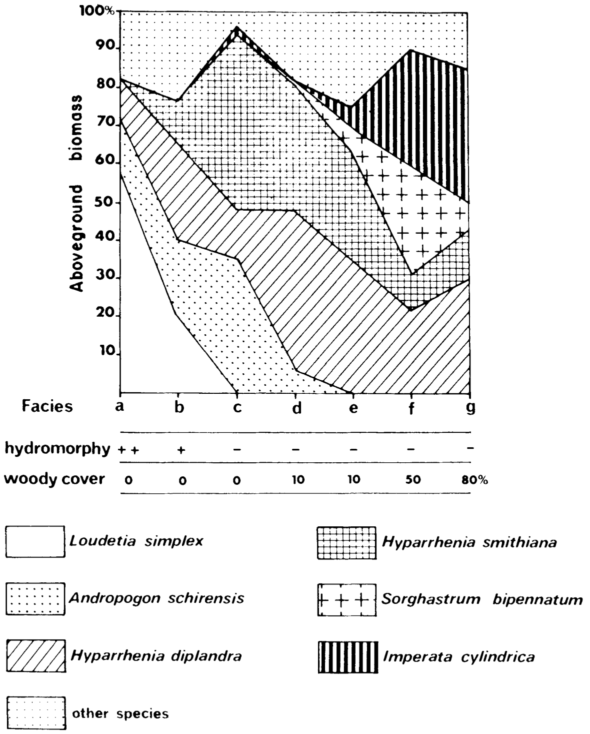


FIG. 2. Respective contribution of the main grasses to the total aboveground biomass in relation to the hydromorphy (soil properties resulting from waterlogging) and woody cover in seven facies. (a) *Loudetia simplex* grass savanna; (b) *L. simplex* intermediate savanna; (c) Andropogoneae grass savanna; (d) Andropogoneae intermediate savanna; (e) Andropogoneae open shrub savanna; (f) Andropogoneae dense shrub savanna; (g) Andropogoneae savanna woodland.

ata cylindrica and *Aframomum latifolium* illustrates this effect. Variations between different facies of the same formation are also due to this interaction. For instance, in the zone dominated by *Andropogon* spp., *Andropogon schirensis* is gradually replaced by *A. canaliculatus* as trees or shrubs appear. The same kind of interference exists between woody elements of the grass layer (seedlings, hemicryptophytes) and the tree layer, thus the heliophilous and sciaphilous facies are easily distinguished.

Life-forms

Although Raunkiaer's (1934) classification of life-forms has often been criticized with regard to its application to tropical plants (see a review of the question in Schnell 1971), it has been used for convenience and completed with additional comments on the growth forms and behavior of the main species in Lamto savannas.

Therophytes are poorly represented. Seeds germinate during the first rains in March but the growth is very slow until August and the seedlings have to compete severely with the rapidly growing perennials. Only one grass (*Sorghastrum bipennatum*), one composite (*Aspilia bussei*), and a few legumes (*Indigofera* spp. and *Tephrosia* spp.) belong to this type. The growth of the legumes is initially prostrate but later they develop a strong aerial system often reaching a height of 2 m (e.g., *Indigofera paniculata*, *Tephrosia bracteolata*) and a basal diameter of 1–2 cm (e.g., *Indigofera* spp.).

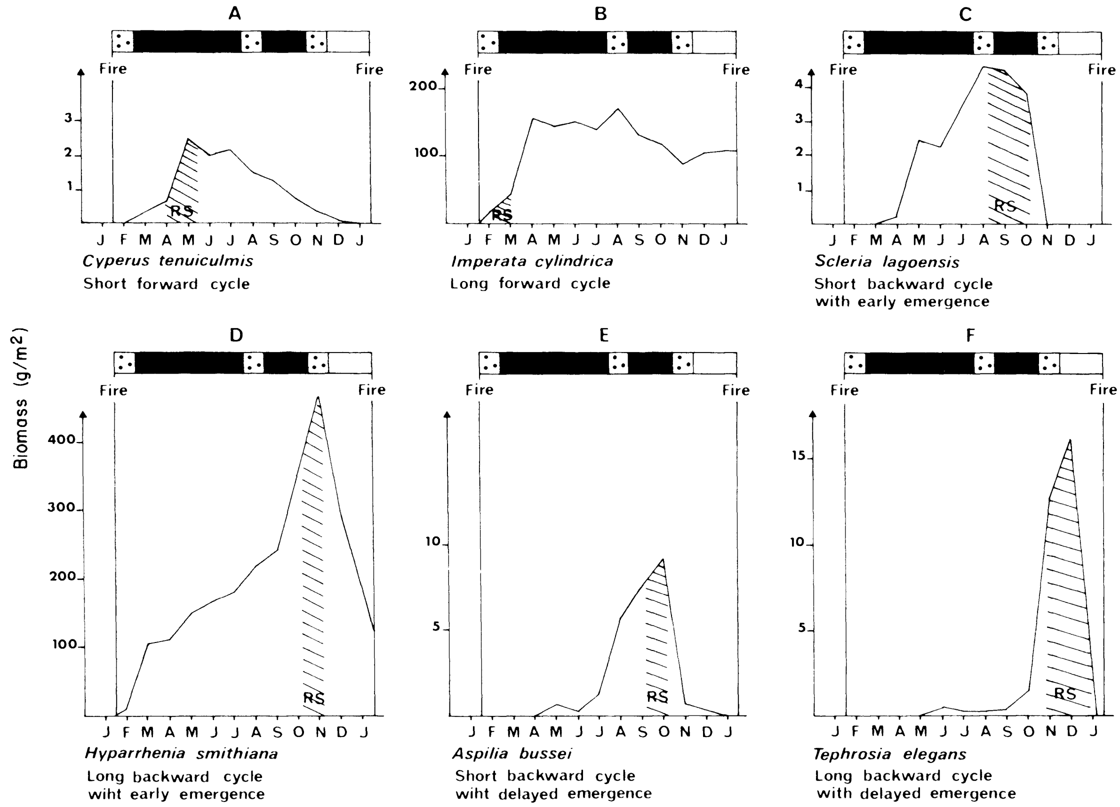
Geophytes provide ideal protection against fire. The underground system is generally replete with reserves and allows rapid growth, flowering, and fruiting soon after burning, even when fire occurs at the height of the dry season. Examples are given by a number of monocots with bulbs (e.g., *Urginea indica*), tubers (e.g., *Eulophia* spp.), or rhizomes (e.g., *Imperata cylindrica*).

Hemicryptophytes are the main type of primary producer. They generally have strong fasciculate roots and regrowth starts rapidly after fire, continuing throughout the wet season until seed formation. Most grasses and sedges belong to this life-form; they are caespitose and tolerate fire due to the dense and tight bases of tillers and leaf sheaves. This results in the irregular mosaic of grass tufts and bare ground more characteristic of the open facies than of closed ones, where tufted hemicryptophytes are partly replaced by therophytes and geophytes, often single-stemmed. A large number of herbaceous dicotyledons is scattered in every facies. Their stems are often prostrate and twining (e.g., *Galactia tenuiflora*, *Rhynchosia sublobata*, *Sphenostylis holosericea*, *Vigna* spp.); a few are erect and, while fire leaves only a calcined skeleton, a exceptional shoot may escape and new buds will appear (e.g., *Indigofera polysphaera*). The root system of such dicots may be very large and as developed as that of a small shrub.

Cochlospermum planchoni, *Cissus doeringii*, *Eriosema psoraleoides*, and *Lippia rugosa* are subligneous bushy species whose aerial systems do not ordinarily tolerate fire; they behave as hemicryptophytes or at the most as low chamaephytes. Their development is basitonic (ramifications on the lower part of the axes) at the beginning but is more or less compensated by a number of weak acrotonic ramifications (on the upper part of the axes). Most trees and shrubs behave as hemicryptophytes during the firest few years of their life but, except for particular individuals of *Piliostigma thonningii* (see below), no woody species are true hemicryptophytes.

Chamaephytes do not survive long in burnt savannas where the only representative is the low-growing *Crossopteryx febrifuga* during its first developmental stages. Other woody species grow almost directly from a hemicryptophyte to a phanerophyte.

Phanerophyte behavior is often perturbed by fire in the first developmental stages and the reactions of the various species and even of the individuals of one species differ greatly from one another. For *C. febri-*



A: *Cyperus tenuiculmis* Short forward cycle

B: *Imperata cylindrica* Long forward cycle

C: *Scleria lagoensis* Short backward cycle with early emergence

D: *Hyparrhenia smithiana* Long backward cycle wiht early emergence

E: *Aspilia bussei* Short backward cycle wiht delayed emergence

F: *Tephrosia elegans* Long backward cycle with delayed emergence

FIG. 3. Biomass cycle of six characteristic herbs to illustrate the different types of phenological cycle. Hatches indicate the reproductive stage (RS) of the species. The upper parts of the graphs represent monthly rainfall: <50 mm: white areas; 50–100 mm: dotted areas; >100 mm: black areas). Forward cycle = flowering soon after emergence; backward cycle = flowering during the second wet season or at beginning of dry season.

fuga, it seems that fire only slows growth. Short annual shoots spring from pollards whose increment is very low; this stage corresponds to a chamaephyte but is transitory, and the architecture and development already resemble those of mature shrubs. *Bridelia ferruginea* is often found as a hemicryptophyte, producing annual, often fruiting suckers. Development occurs when a long, thick shoot tolerates the fire and ramifies. Otherwise, the plant dies after a few years; it seems that the superficial and thin root system does allow the plant to survive for long at this stage. During its first developmental stages, *Cussonia barteri* also behaves as a hemicryptophyte producing annual, never fruiting shoots from a fast-growing taproot. A single tolerant shoot later develops and the others disappear. Similar to the above species, *Piliostigma thonningii* appears as a microphanerophyte with a transitory behavior. However, many individuals of this species may be considered true hemicryptophytes. The underground system develops a strong taproot with perennial plagiotropic underground shoots (not rhizomes) whose buds are at ground level and produce a large number of annual suckers, otten with a complete reproductive cycle. This form seems stable and occurs with phanerophytes in apparently similar ecological conditions.

Fire results in a periodic reduction of shoot growth and most species take a bushy form in their first years of development with the basal multiplication of annual, then perennial shoots. Later, the shoots escaping the fire change their branching during growth and the species acquire their final architecture. In unburnt areas, the behavior of herbaceous or woody species is not greatly modified, at least after 15 yr of protection against fire. Woody species grow faster than in burnt savannas but their transitory developmental stages still occur. These are shortened but the withering of annual shoots remains for most species. A number of individuals of *P. thonningii* are still found as hemicryptophytes, and some species such as *Ficus capensis*, *F. vallis-choudae*, or *Nauclea latifolia* nearly always retain a bushy form although they may become trees even in burnt savannas. Some species which are usually robust in burnt savannas are often weak in protected areas. Absence of fire might perturb some of them by maintaining a dense layer of standing dead material impeding the growth of young suckers (e.g., *Annona senegalensis*) and some others by keeping

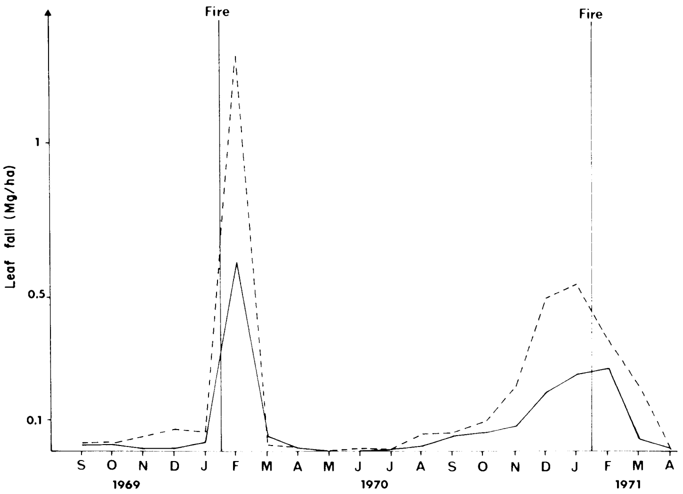


FIG. 4. Monthly leaf fall on an open facies (solid line) and a dense facies (broken line) during two consecutive years to illustrate the interannual variability.

alive buds whose opening on old axes would weaken the plant (e.g., *Borreria octodon*, *Desmodium ramosissimum*).

In burnt or protected areas, herbaceous and woody species have large root systems, which illustrates their reaction to drought. (Fire principally increases the effects of drought.) Resistance to unfavorable conditions is thus ensured and a large part of productivity occurs belowground.

Phenological cycle

The annual cycle of the vegetation is controlled by the dry season which occurs from December to January: the vegetation withers, annuals die, and leaf fall occurs. Fires occur at the height of the dry season (end of January) and only make this rhythm more extreme than in unburnt areas where leaf fall spreads over several weeks. A rapid regrowth and a first wave of flowering of the herbaceous species occur even before the onset of the rains. During the main wet season (March–July), the vegetative growth goes on and woody species flower. A drier period occurs in August but the vegetation generally does not seem to suffer from it. The main wave of flowering occurs during the little wet season (October–November); growth then stops and withering starts.

The behavior of the herbaceous species varies according to the date of emergence (early or delayed), the date of flowering (forward or backward cycle), and the length of the vegetative state (César 1971). Six types of herbaceous producers have thus been defined (Fig. 3). Plants with a forward cycle flower soon after their emergence, which occurs either immediately after fire or with the first rains. The cycle may be short; the aboveground parts wither rapidly and have disappeared when the dry season occurs (e.g., *Cyperus tenuiculmis*, Fig. 3a). The cycle may be long and the aboveground parts last until next burning (e.g., *Imperata cylindrica*, Fig. 3b). Most plants with a forward cycle are geophytes whose large root systems allow a rapid regrowth at the end of the dry season. They sometimes flower even before the spring of their first vegetative shoots and all have spread their seeds before being covered by the grass layer. Plants with a backward cycle flower during the second wet season and even at the beginning of the dry season; flowering coincides with the maximum vegetative development. Their emergence may be early in spring and their cycle short (e.g., *Scleria lagoensis*, Fig. 3c) or long as in most caespitose hemicryptophytes that provide the largest amount of fuel to the fire (e.g., *Hyparrhenia smithiana*, Fig. 3d). They take advantage of a strong root system supplying regrowth at the beginning of the wet season. The delayed emergence group is composed of therophytes. They germinate during the main wet season but often grow during the second one. Their cycle may be short (e.g., *Aspilia bussei*, Fig. 3e) or long (e.g., *Tephrosia elegans*, Fig. 3f). Life-form and type of cycle are closely related and give homogeneous functional groups; these help in interpreting the production cycles of the various facies.

The phenological behavior of the woody species is more homogeneous, at least for leaf outbreak and leaf fall. Some differences in the flowering dates are noticed between species. Some are very irregular and no clear pattern has been observed for *Cussonia barteri*. Low species such as *Annona senegalensis* flower and fruit before being covered by the grasses. *Bridelia ferruginea* often flowers with very few leaves. In contrast, *Piliostigma thonningii* is late and flowers still occur at the beginning of the dry season. Leaf fall occurs almost at the same time for all the species on all facies, but time and duration vary considerably between years (Fig. 4). Leaf litter has been collected during two complete cycles (February 1969–February 1971) and less accurate data (samplings just before and after fire) were obtained in 1973, 1975, and 1978. Leaf fall may occur almost completely after fire (up to 90%) or may start from July onwards with only 25% of the leaves falling after fire. Hopkins (1966) and Collins (1977) working in Nigeria on comparable savannas, have stressed the high seasonality of leaf fall; Hopkins, however, pointed out the variations in the falling pattern from year to year. They obtained figures close to those from corresponding sites in Lamto (≈ 1 and 2 Mg·ha^{-1}·yr^{-1}). No clear relation has been found with the climatic cycles within the same period. These variations have important ecological implications since most of the leaves falling before the fire are burnt and do not participate in the turnover of organic matter.

ANALYSIS OF VEGETATION BIOMASS

Sampling method

Only one site per facies could be studied for primary productivity measurements. Nine facies (7 burnt, 2 unburnt) had to be studied and the available means did not allow for replication of the sites. However, the representativeness of the sites has been tested in each facies through detailed floristic inventories and structural analyses of the herbaceous layer (Poissonet and César 1972, César and Menaut 1974).

In each representative site, the number of plots acceptable for biomass measurements has been estimated through the graphic method of the successive means (Greig-Smith 1964). This number varied from one facies to another between 8 and 16 quadrats. The size of each quadrat, 1 m^2, was assumed to be large enough to cover the heterogeneity of tussock distribution. Harvest data from these quadrats gave standard errors of the means ranging from 4 to 10% with a mean of 7.2%, i.e., an average confidence interval of 15.3% ($P < .05$).

It was decided to harvest each month, from each facies, 16 quadrats randomly selected from among the 192 that composed a site. During the entire study, the confidence intervals ($P < .05$) varied between 6.5 and 24.4%, with a mean of 15.7%, according to the facies and the vegetative stage of the herbaceous layer. Species were immediately sorted (living and standing dead matter); the absence of humus on the soil surface enabled an easy harvest of the litter on the ground. Samples were weighed fresh and oven dried to a constant mass at 95°C.

Roots could not be sampled with such accuracy. The hardness of the soil in the dry season and the occurrence of gravels forbade the use of a drill or core extractor. Blocks of soil (20 × 20 cm) were extracted every 10 cm down to 1 m. As this method is very destructive and time consuming, only four quadrats could be sampled at random, each month in each site, among the 16 that were harvested aboveground. No statistical test was used but deviations from the mean ranged from 15 to 69%, with an average of 39.1%; variations depended on the facies, the vegetative stage, the location of the sample with respect to tuft distribution, and the depth of the sample. The root systems were washed free of soil on sieves with meshes 2 mm wide. Living and dead roots were separated in the samples collected in only one quadrat each month for each facies. Samples were weighed fresh and oven dried to a constant mass at 95°C. The accuracy of root sampling is very low and root production data should be considered as broad estimates.

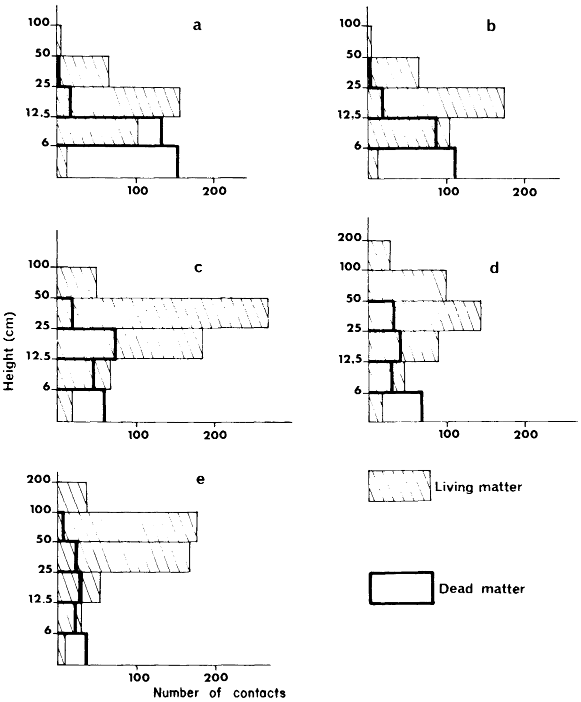


FIG. 5. Biovolume stratification (expressed in number of contacts for 100 points) of living and dead matter in the herb layer of five facies. (a) *Loudetia simplex* grass savanna; (b) Andropogoneae grass savanna; (c) Andropogoneae open shrub savanna; (d) Andropogoneae dense shrub savanna; (e) Andropogoneae savanna woodland.

Herbaceous plants

Stratification of the vegetal matter.—The vertical distribution of aboveground matter has been studied through the measurement of biovolumes by the point contact method (Poissonet and César 1972). The standing dead matter is always densest near the ground but the distribution of the living matter depends on the density of the woody cover. The aboveground biomass is similarly distributed in the two types of grass savanna; $\approx$80% of the biovolume is concentrated in the lower 25 cm (Fig. 5a, b). The occurrence of shrubs and trees modifies this distribution:

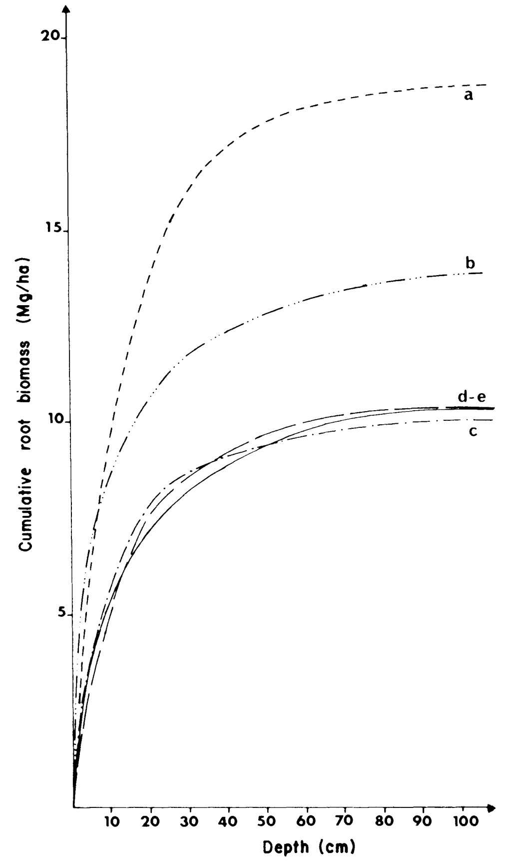


FIG. 6. Root biomass distribution of herbs according to depth in the soil of five facies. (a) *Loudetia simplex* grass savanna; (b) Andropogoneae grass savanna; (c) Andropogoneae open shrub savanna; (d) Andropogoneae dense shrub savanna; (e) Andropogoneae savanna woodland.

the volume of the living matter tends to increase upwards with the density of the woody cover. In the open shrub savannas, ≈90% of the biovolume occurs in the lower 50 cm with a maximum (45%) between 25 and 50 cm (Fig. 5c). In the dense shrub savannas, the maximum still occurs at the same height but 30% of the biovolume occurs between 50 and 200 cm (Fig. 5d). The herbs grow higher in savanna woodlands; the maximum is between 50 and 100 cm and 45% of the biovolume is above 50 cm (Fig. 5e).

Underground, the cumulative values of biomass with depth are represented by a curve rapidly tending toward an horizontal asymptote (Fig. 6); the ordinate of the asymptote represents the theoretical total underground biomass. In any savanna, >80% of the root biomass is concentrated in the upper 30 cm; beyond this depth, the biomass decreases very quickly. In contrast with the aboveground matter, the type of distribution of the roots is not affected by the density of shrubs and trees; total root biomass is remarkably constant in the wooded savannas but increases in grass savannas according to edaphic conditions.

Biomass cycle.—Table 1 summarizes the data obtained for the main biomass components in seven types of burnt savanna. For the aboveground parts, the differences in total biomass are less significant indicators of the functioning of each type of savanna than are the relative proportions of living and dead matter. However, these data do not allow differentiation of *Loudetia* grass savannas from Andropogoneae open shrub savannas for example, and it is necessary to follow the biomass components throughout a cycle. Figure 7 represents the cycle of the aboveground living, dead, and total dry matter in four facies. It is also interesting to study the contribution of each species, as small variations in the substrate are likely to modify greatly the proportions of species biomasses without changing the floristic composition and total biomass. The estimation of all the biomass components gives a good indication of local or temporary variations in soil fertility (César 1973).

Andropogoneae grass savannas have the highest aboveground living biomass (annual mean = 4.4 Mg/ha); in other facies, this biomass is 3.2–3.6 Mg/ha. Growth is also faster in the grass savanna and the maximum biomass is reached in October after which

TABLE 1. Above- and belowground herb biomass (megagrams per hectare) in seven facies: (a) *Loudetia simplex* grass savanna; (b) *L. simplex* intermediate savanna; (c) Andropogoneae grass savanna; (d) Andropogoneae intermediate savanna; (e) Andropogoneae open shrub savanna; (f) Andropogoneae dense shrub savanna; (g) Andropogoneae savanna woodland.

	Facies						
	a	b	c	d	e	f	g
	Herb biomass (Mg/ha)						
Aboveground parts							
Mean living matter biomass	3.5	3.6	4.4	4.1	3.4	3.3	3.2
Mean dead matter biomass	0.7	0.8	1.0	1.3	0.8	1.0	1.4
Mean total biomass	4.2	4.4	5.4	5.4	4.2	4.3	4.6
Maximum total biomass	6.9	7.0	9.9	11.1	7.0	8.3	6.9
Belowground parts							
Mean biomass	19.0	19.0	13.8	10.5	10.1	10.5	10.5
Maximum biomass	23.5	28.8	21.2	17.5	14.3	16.3	16.8

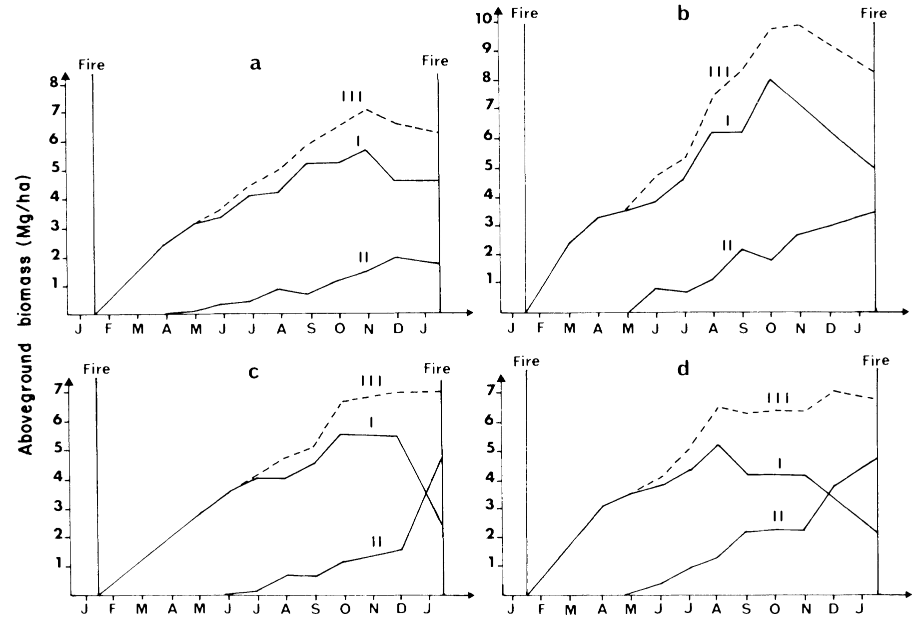


FIG. 7. Aboveground biomass cycle of the herbaceous layer in 1970 (I, living matter; II, dead matter; III, total dry matter). (a) *Loudetia simplex* grass savanna; (b) Andropogoneae grass savanna; (c) Andropogoneae open shrub savanna; (d) Andropogoneae savanna woodland.

flowering occurs and biomass quickly decreases (Fig. 7b). These savannas profit from the optimum conditions for the development of the grass layer. Most roots are in the upper 30 cm where the soil has a good texture and structure and where the nutrient conditions are sufficient for good grass development; at lower depths a concretionary horizon impedes root penetration and prevents the development of shrubs and trees. On the other facies, herb production is limited either by poor soil (hydromorphic pseudogley) or by competition with woody plants. In *Loudetia* savannas, the increase in living biomass is regular until November when it is maximum (Fig. 7a). This type of savanna, and especially the predominant species *Loudetia simplex*, suffer little from drought: the living biomass decreases little after fructification and during the dry season. When fire occurs, dead matter constitutes only 25% of the total biomass and this explains why *Loudetia* savannas burn with more difficulty than others. In Andropogoneae shrub savannas, the living matter remains constant throughout the period of flowering and fruiting until December and then sharply decreases before burning (Fig. 7c). Maximum living biomass is reached very early in savanna woodlands and slowly decreases from August onwards (Fig. 7d). In wooded savannas, dead matter is specially augmented at the onset of the dry season; it exceeds living matter and constitutes ≈70% of the total biomass when fire occurs. Despite the increase of the water content of living grasses with the woody cover (50% in dense savannas vs. 30% in *Loudetia* grass savannas), burnings are always more severe in wooded savannas with a thicker litter layer than in grass savannas, thus preventing the establishment of a forest flora.

The underground biomass cycles observed in grass and shrub savannas are rather similar (Fig. 8). After burning, root biomass decreases; the roots partly die but the decrease seems mainly due to translocations of food reserves from the roots to the growing shoots. The early development of absorptive rootlets rapidly compensates for these translocations and root biomass increases. Growth may be stopped at any dry period

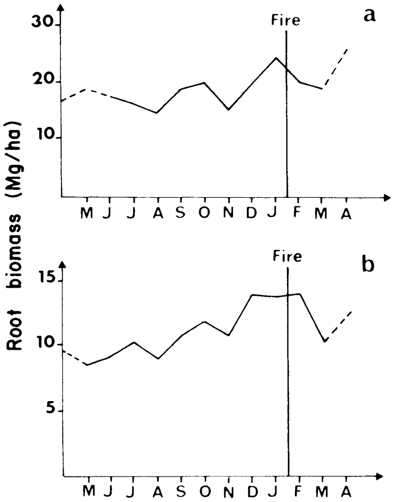


FIG. 8. Underground biomass cycle of the herbs in (a) *Loudetia simplex* savannas (mean of two facies) and (b) Andropogoneae shrub and tree savannas (mean of three facies).

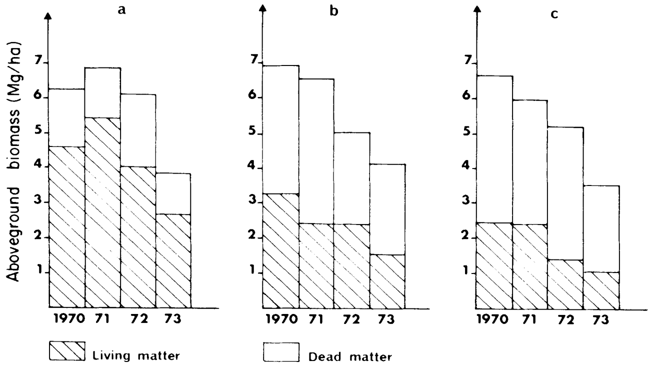


FIG. 9. Variation of herbaceous biomass (living and dead matter) at the end of the cycle during four consecutive years in three facies. (a) *Loudetia simplex* grass savanna; (b) Andropogoneae grass savanna; (c) Andropogoneae savanna woodland.

during the year and, in all facies, changes in underground biomass are more abrupt than those of the aboveground biomass. At the onset of the dry season, root biomass is maximum due to the accumulation of food reserves. In all the savannas, underground biomass is always higher than aboveground biomass, especially in *Loudetia* savannas (deep sandy soils) where root biomass is nearly twice that of the others. In Andropogoneae savannas, the absence of woody plants seems to favor root development as it does for the aboveground parts: the grass facies has the highest biomass (14 Mg/ha as compared to 10–11 Mg/ha in other facies).

Types of biomass cycle do not change much from year to year but large differences are noticed in the values of the different components of the biomass. The aboveground biomass at the end of the cycle decreased by ≈50% from 1970 to 1973 because the shortage of water in 1969 was probably not restored during the following years (Fig. 9). Root biomass also decreased, e.g., from 19 to ≈7 Mg/ha in *Loudetia* savannas. The underground system seems more affected by unfavorable conditions than the aboveground parts. The amplitude of the variations observed within a cycle and between years shows the necessity of studying the different components of herb production at the same time, during the same cycle.

Estimate of production.—Calculation of production is complicated since it is necessary to combine several phenomena such as animal comsumption, decay of dead matter, and exchanges between above- and belowground organs. These components are difficult to estimate with accuracy in Lamto savannas and the data presented here give only an imperfect estimate of production.

Special attention has been paid to the decay of living and dead matter of above- and belowground parts. Compared with living matter, the amount of dead matter measured in the field is underestimated in variable proportions according to species and environment. This proportion may be represented by a coefficient of loss at death of green parts (α), expressing both the drying of the living matter and part of the transfers from the leaves to the roots. Thus, an amount of litter (L) collected in the field comes from the withering of an amount of living matter (V), in the ratio $L/V = \alpha$, where L and V are in dry weights. This coefficient has been calculated for the main savanna species: *Hyparrhenia diplandra*, $\alpha = 0.46$; *Andropogon canaliculatus*, 0.56; *Imperata cylindrica*, 0.57; *Loudetia simplex*, 0.67. From knowledge of the specific composition and the biomass structure, α has also been estimated for the main facies: *Loudetia* grass savanna, $\alpha = 0.61$; Andropogoneae grass savanna, 0.50; Andropogoneae shrub savanna, 0.52; Andropogoneae savanna woodland, 0.52. The rate of decomposition of leaf litter has been determined by the Wiegert-Evans (1964) method and its modification by Lomnicki et al. (1968). Harvests of living and dead matter were done at fortnightly intervals on the assumption that no material would disappear within that period. In *Loudetia* savannas, the mean monthly disappearance rate is 7.6% and reaches 12% in Andropogoneae savannas.

Consumption has been estimated through the study of the energy budget of the main animal groups (Lamotte 1977). Due to the quasi-absence of grazing mammals, annual consumption reaches only ≈10% of the aboveground production. Studying the seasonal variations of the nitrogen, phosphorus, and potassium content of *Loudetia simplex*, P. Villecourt, W. Schmidt, and J. César (*personal observation*) have found that 1.9 Mg/ha of dry matter was migrating from the shoots after fruiting. However, these data are difficult to interpret, owing to the lack of knowledge of the plant physiology and to the low accuracy of root production estimates.

Adding the losses to the biomass increment provides an estimate of the aboveground production and its annual cycle. Table 2 summarizes production data from seven facies and Fig. 10 represents the production cycle in three main types of savanna. The species with early emergence grow rapidly after fire, probably due

TABLE 2. Above- and belowground production (megagrams per hectare per year) of the herbs in seven facies. Six types of producers are distinguished for the aboveground parts; belowground, species could not be separated and data are given in relation to the season.

	Loudetia simplex grass savanna	*L. simplex* intermediate savanna	Andropogoneae grass savanna	Andropogoneae intermediate savanna	Andropogoneae open shrub savanna	Andropogoneae dense shrub savanna	Andropogoneae savanna woodland
				Aboveground production ($Mg \cdot ha^{-1} \cdot yr^{-1}$)			
Short forward cycle	0.06	0.13	0	0.02	0.64	0.56	0.11
Long forward cycle	0.37	0.56	0.06	0.07	1.21	5.24	5.19
Short backward cycle with early emergence	0.12	0.70	0.01	0.04	1.39	0.49	0.08
Long backward cycle with early emergence	7.76	7.76	15.34	14.79	8.83	5.10	7.80
Short backward cycle with delayed emergence	0	0	0.02	0	0.63	4.72	1.22
Long backward cycle with delayed emergence	0	0	0.01	0.01	0.06	0.03	0.07
Total aboveground production	8.3	9.2	15.4	14.9	12.8	16.1	14.5
				Belowground production ($Mg \cdot ha^{-1} \cdot yr^{-1}$)			
February–July	3.96	4.49	4.49	7.41	...	2.91	5.37
August–October	3.17	4.62	5.51	4.94	...	2.18	3.90
November–January	6.07	4.09	10.40	6.65	...	5.31	2.93
Total belowground production	13.2	13.2	20.4	19.0	13.3	10.4	12.2
Total production	21.5	22.4	35.8	33.9	26.1	26.5	26.7

to translocations from the roots; then production decreases until April–May when the wet season is established and growth conditions are optimal. In *Loudetia* savannas, production is very regular until seed formation and the end of the vegetative activity (Fig. 10a); a peak occurs in August in Andropogoneae grass savannas (Fig. 10b). In the grass savannas, almost all the production comes from hemicryptophytes with a long backward cycle. The importance of this type of producer decreases with the woody cover, which promotes the diversification of the production spectrum of dense shrub savannas by introducing shade-tolerant and more exacting species; the polymodal curve of production indicates the activities of the different groups of producers (Fig. 10c).

Underground parts have not been so accurately studied and the different species have not been separated; the results are only rough estimates. Nevertheless, root production cycles can be expressed in relation to season (Table 2) and depth (Table 3). Annual root production is maximum (≈20 Mg/ha) in Andropogoneae grass savannas where the annual turnover rate (production/maximal biomass) reaches 100%. Root production remains between 10 and 13 Mg/ha in other savannas, but the turnover rate is higher in wooded savannas (77%) than in *Loudetia* savannas (51%). Underground production becomes less than the aboveground production in wooded savannas, contrary to the biomass.

Total herbaceous production is low in *Loudetia* grass savannas (poor soil), medium in Andropogoneae shrub and tree savannas (competition with woody plants), and maximum in Andropogoneae grass savannas.

Woody plants

A dimension analysis was done on 40 individuals of each of the four main species; they were cut, their woody root system excavated, and all the components weighed as dry matter. Correlations have been found between the weight of leaves, twigs, branches, stems, and roots, and the height, diameter at breast height, and crown surface (Menaut 1971). Charts were established to determine the biomass of the various components of each individual measured in the plots. Thus, the overall leaf, branch, stem, and root biomass are easily estimated for the main facies (Table 4). The very low value of the leaf area index (0.1–1) and the ratio of leaf weight to total biomass (2–5%) explain the low productivity of the woody plants. Root systems are well developed and constitute ≈30% of the total biomass. Variation in biomass was calculated from direct growth measurements of all the individuals on

TABLE 3. Production cycle of herb roots according to their depth in a savanna woodland where *Imperata cylindrica* predominates.

	Root production $Mg \cdot ha^{-1} \cdot yr^{-1}$				
Depth (cm)	0–10	10–20	20–40	40–80	Total
May–July	0.91	1.42	0.73	2.61	5.67
August–October	1.76	0.52	0.76	0.96	4.00
November–January	1.28		0.74	0.44	2.46

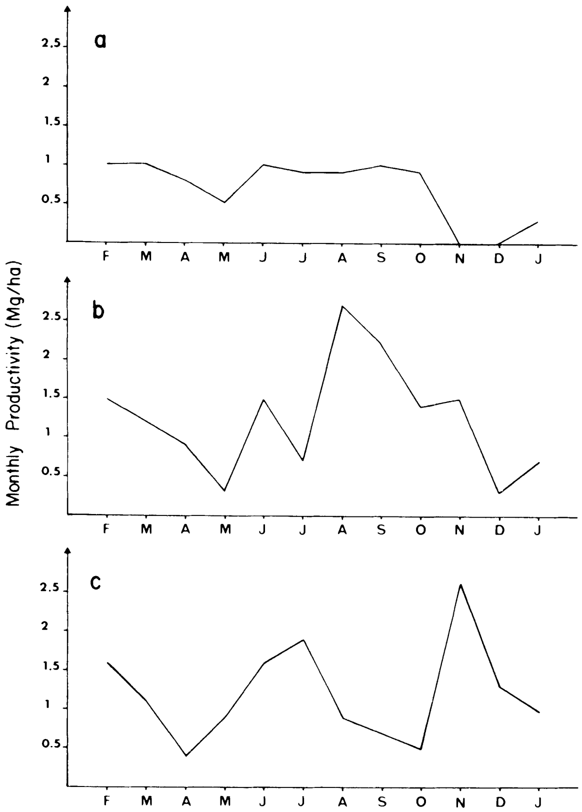


FIG. 10. Annual cycle of herbaceous production in three facies to illustrate the activities of the different groups of producers. (a) *Loudetia simplex* grass savanna; (b) Andropogoneae grass savanna; (c) Andropogoneae savanna woodland.

each plot. For savanna shrubs and trees, only a rough estimate of the age is possible; growth rings are difficult to read and their interpretation is very doubtful. Further, burning increases the differences between growth processes of above- and belowground parts from one plant to another. The first growth measurements were made in 1970 and later ones in 1972, 1973, and 1975.

The more youthful the plants and the more they are influenced by fire, the wider the individual and interannual growth variations. The growth increment is much less irregular for mature plants of the upper strata and it is possible to estimate their mean annual girth increment. These are (in cm/yr): *Piliostigma thonningii*, 0.5; *Crossopteryx febrifuga*, 0.6; *Bridelia ferruginea*, 0.9; and *Cussonia barteri*, 2.4 (Menaut 1977*a*). The annual production of shoots and the fall of terminal twigs are very sensitive responses to ecological conditions and the amplitude of their variations makes utilization of height measures difficult. It seems more justified to use height classes instead of actual values. These allow broad estimates of height growth for the main savanna species of the shrub layer (2–8

TABLE 4. Biomass of leaves (L), branches (B), stems (S), and roots (R) of the woody species in five facies.

	Loudetia simplex grass savanna				Andropogoneae savannas															
					Intermediate savanna				Open shrub savanna				Dense shrub savanna				Savanna woodland			
Density of woody species (plants per hectare)					120				160				300				800			
Cover					7%				15%				20%				45%			
Leaf area index					0.1				0.2				0.4				1			
	L	B+S	R	Total	L	B+S	R	Total	L	B+S	R	Total	L	B+S	R	Total	L	B+S	R	Total
	Biomass (kg/ha)																			
Canopy height																				
0–2 m	3	3	30	36	5	10	30	45	8	12	60	80	16	25	260	300	50	80	580	710
2–8 m	6	25	25	56	300	7400	3600	11 300	600	16 800	7700	25 100	1600	28 600	12 800	43 000	2100	25 600	14 800	42 500
>8 m									100	5100	1400	6600	100	4000	1200	5300	1700	28 600	11 200	41 500
	Total biomass (Mg/ha)																			
					0.3	7.4	3.6	11.3	0.7	21.9	9.2	31.8	1.7	32.6	14.3	48.6	3.8	54.3	26.6	84.7

TABLE 5. Biomass increment (megagrams per hectare) of branches, stems, and roots of the woody species in four facies.

	Intermediate savanna			Open shrub savanna			Dense shrub savanna			Savanna woodland		
Stratum	Branches and stems	Roots	Total	Branches and stems	Roots	Total	Branches and stems	Roots	Total	Branches and stems	Roots	Total
					1970 Biomass (Mg/ha)							
2–8 m	7.40	3.60	11.0	16.8	7.7	24.5	28.6	12.8	41.4	25.6	14.8	40.4
>8 m				5.1	1.4	6.5	4.0	1.2	5.2	28.6	11.2	39.8
Total	7.40	3.60	11.0	21.9	9.1	31.0	32.6	14.0	46.6	54.2	26.0	80.2
					1973 Biomass (Mg/ha)							
2–8 m	7.75	3.75	11.5	17.7	8.1	25.8	27.1	12.2	39.3	25.9	15.0	40.9
>8 m				5.2	1.4	6.6	6.8	2.5	9.3	30.6	12.2	42.8
Total	7.75	3.75	11.5	22.9	9.5	32.4	33.9	14.7	48.6	56.5	27.2	83.7
Biomass increment in 3 yr (Mg/ha)	0.35	0.15	0.5	1.0	0.4	1.4	1.3	0.7	2.0	2.3	1.2	3.5
Mean annual increment (%)	1.6	1.4	1.5	1.5	1.5	1.5	1.3	1.6	1.4	1.4	1.5	1.5

m). During 5 yr, *Crossopteryx febrifuga* and *P. thonningii* have not shown any appreciable height increase; the mean growth of *B. ferruginea* and *Cussonia barteri* was 5 and 11 cm/yr, respectively. *Crossopteryx febrifuga* and *P. thonningii* have the slowest girth and height growth; *B. ferruginea* and especially *Cussonia barteri*, a softwood species, have a more conspicuous and regular growth.

Table 5 summarizes biomass increment data between 1970 and 1973 for four facies. Data on woody plants 0–2 m tall have not been included; variations in above- and belowground perennial biomass are negligible compared with those of other woody elements. The mean biomass increment is ≈1.5%. It varies little between aerial parts and roots and between various facies; differences are not significant and require further study. The dynamics of a facies might be more accurately defined by the analysis of wood biomass variations in both upper layers than by structural analysis. For instance, tree biomass variations are slight in open facies and do not seem bound to the evolution of the shrub layer. In some dense facies, increase in tree biomass may partly result from growth by some individuals out of the shurb layer. Consequently the shrub layer biomass decreases and the facies could evolve towards a tree savanna, though this might just be a fluctuation.

Litter from bark, branches, and dead plants has to be added to biomass increment. This litter is rather difficult to estimate. For a species such as *Crossopteryx febrifuga*, a variable but not negligible part of the heartwood of branches and stems is partly decomposed and eaten or collected by termites. Wood fall is less seasonal than leaf fall and is extremely irregular during the year. Dead branches and twigs remain on the stem for a long time and most often fall accidentally during storms. Moreover, a part is burnt in place before falling. The wide heterogeneity of the present results dictates that observations must be continue for a long time.

The annual production of leaves and green shoots has been estimated in each facies from specific correlations. Results have been confirmed by litter harvests which gave values ≈20% lower, corresponding to the loss of dry weight of leaves before abscission (Bray and Gorham 1964). Carried over several cycles, litter harvests have emphasized the importance of interannual variability and also that values obtained by calculation were only valid for the year when measures were taken (Menaut 1974). Variations in esti-

TABLE 6. Production of the woody species in four facies.

	Intermediate savanna	Open shrub savanna	Dense shrub savanna	Savanna woodland
Aboveground biomass	7700	22 600	34 300	58 200
Belowground biomass (kg/ha)	3600	9200	14 300	26 600
Leaves and green shoots	430	1000	2380	5530
Aboveground biomass increment	120	330	420	760
Belowground biomass increment (kg·ha^{-1}·yr^{-1})	50	130	230	370
Total net production (Mg·ha^{-1}·yr^{-1})	0.6	1.5	3.0	6.7

TABLE 7. Total net production (megagrams per hectare per year) of the herbaceous and woody species in seven facies of Lamto savannas.

	Loudetia savannas				Andropogoneae savannas									
	Grass savanna		Intermediate savanna		Grass savanna		Intermediate savanna		Open shrub savanna		Dense shrub savanna		Savanna woodland	
	Herbs	Woody species	Herbs	Woody species	Herbs	Woody species	Herbs	Woody species	Herbs	Woody species	Herbs	Woody species	Herbs	Woody species
	Production ($\mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$)													
Aboveground	8.3	0	9.2	0	15.4	0	14.9	0.55	12.8	1.4	16.1	2.8	14.5	6.3
Belowground	13.2	0	13.2	0	20.4	0	19.0	0.05	13.3	0.1	10.4	0.2	12.2	0.4
Sub-total	21.5	0	22.4	0	35.8	0	33.9	0.6	26.1	1.5	26.5	3.0	26.7	6.7
Total	21.5		22.4		35.8		34.5		27.6		29.5		33.4	

mates of production of leaves and green shoots of low woody plants are very wide since these are directly affected by fire, the effect of which is highly variable between places and years. Interannual variability plays an even more important part as green material makes up most of the total annual production of woody plants (Table 6).

Total net production

Table 7 summarizes various components of total annual net production of herbs, shrubs, and trees in the main facies. Even though herbaceous plants are only a small part of the aboveground biomass, they may make up nearly all the aboveground net production. It is only in the densest facies that the production of woody plants reaches 10–20% and these facies cover only a small area at Lamto.

Leaf production of woody plants should not be underrated. This material plays a major role in the savanna when the environmental conditions are the most unfavorable. When the litter and the herb layer have been removed by fire, the topsoil is laid bare and subject to extreme heating and drying. In shrub and tree savannas, leaf fall after fire produces a litter layer protecting soil and litter fauna. These leaves also are the only source of consumable vegetal matter at this time and are decomposed as soon as the first rains occur.

CONCLUSIONS

The few results available from similar savannas are difficult to compare because of the lack of details on the functioning of these ecosystems (Menaut 1979). However, the *Trachypogon* llanos in Venezuela have an aboveground productivity ($9.1\ \mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$) close to that of the *Loudetia* grass savannas (San José and Medina 1977); in India, the *Cynodon* and *Dichanthium* savannas of Varanasi are somewhat more productive than the Andropogoneae savannas of Lamto (Singh 1972). In West Africa, the quantitative data given by Egunjobi (1974) for Guinea savannas in Nigeria are very similar to those of Lamto and the thorough research of Hopkins (1968, 1970) has shown that the "derived" savannas of Nigeria have a structure and a functioning very close to that of Lamto.

Fire is an essential component of this type of savanna by its effects upon the flora and vegetation dynamics and also by its major role in the energy budget of the ecosystem. In different tallgrass savannas, it seems that fire burns the same proportion of aboveground production. In the dry savannas of the Serengeti National Park (Tanzania), bush fires destroy 53% of the aboveground production (Sinclair 1975); in the humid savannas of Lamto where the absence of large mammals is balanced by the herbivorous invertebrates, the saprophages and the decomposers, the average value is 57%. Whatever the consumers may be, they abandon to the fire the same percentage of aboveground production; it is interesting to note that the large mammals do not make better use of the primary production than do the small consumers and decomposers.

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