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Stocks of nitrogen in vegetation and soil in West African moist savannas and potential effects of climate change and land use on these stocks

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Abstract. Moist savannas which include undifferentiated moist woodlands and savannas with abundant *Isoberlinia doka*[1] and *I. tomentosa* (also known as Sudanian woodlands and Guinea–Congolian secondary grassland and wooded grassland) extend across West Africa up to the Central African Republic. Nitrogen stocks in the standing woody vegetation, litter and soil as well as the amounts of nitrogen transferred between these stocks and that lost through savanna burning of woodland and open moist savanna types are presented. Most of the total nitrogen is in the soil and then in the woody vegetation, with the least amount in the herbaceous vegetation. In a global change scenario characterized by elevated carbon dioxide levels and increased temperatures, it is predicted that there may be a reduced grass abundance and an increased woody species cover. However, human induced land use changes usually drastically reduce woody plant numbers. It is therefore predicted that forbs and low shrubs may dominate the future vegetation of moist savannas. The implications of such vegetation changes on nitrogen stocks are discussed.

Key words. Nitrogen cycling, moist savanna, West Africa, global change.

INTRODUCTION

Savanna is defined as seasonal tropical vegetation in which there is a closed or nearly closed cover of grasses that are at least 80 cm high with flat, cauline leaves and in which trees and shrubs are most often present (Sanford & Isichei, 1986). Savanna vegetation is usually burnt annually. In West and Central Africa north of the equator, two savanna systems may be distinguished: (1) Sudan-type savannas in a sub-humid climate which are derived from the degradation of dense dry forest and woodland, equivalent to Sudanian woodland with abundant *Isoberlinia* (White, 1983); (2) Guinea-type savanna in a humid climate which has replaced moist, semi-deciduous forest (UNESCO, 1979)—the forest/savanna transition or 'Guinea-Congolian secondary grassland' of White (1983). These two formations, located in the ecoclimatic zone where moisture-indexed length of the growing season is between 151 and 270 days, constitute moist savannas, the area where the present study was carried out (Figs 1 and 2). Savannas cover about 12.3 million ha in Africa, 42.3% of the continent's land area, and more than 80% of West Africa is savanna of which moist savannas make up a substantial part.

The long-term objective of Global Change and Terrestrial Ecosystems (GCTE) Focus 1 (Ecosystem Physiology), Activity 1.2: Changes in Biogeochemistry, is to determine the interactive effects of land use, altered atmospheric composition and climate change on the biogeochemical cycles of carbon, nitrogen and other elements. The overall emphasis of the biogeochemistry activity is the understanding of the terrestrial regulation of element pools, transformations, gains and losses as they are altered by the components of global change (Kristiansen, 1993).

Mineral nutrients are most important, next to water, in limiting primary production in West African moist savannas. Of these mineral nutrients, nitrogen has been found to be most often limited, necessitating a clear understanding of its cycling. Rastetter *et al.* (1992) have also observed that under conditions of increased temperature and carbon dioxide levels, interactions between carbon and nitrogen cycles have ramifications on a diversity of ecosystem properties, from tissue function to whole ecosystem carbon storage. They observe further that the distribution of carbon, nitrogen and other elements between vegetation and soils is one of the biogeochemical properties that explain changes in carbon storage in terrestrial ecosystems. We began a study of nitrogen cycling in savanna ecosystems as part of the Nigerian Man and Biosphere Project (see Isichei, 1983) but feel that some of the results are applicable to some of the thrusts of the GCTE research. Nitrogen accumulation by the major grasses in the sites used for the present study has been reported (Isichei, 1983) but the

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[1] Species nomenclature is after Hutchinson & Dalziel (1954) as revised by Keay & Hepper (1972)

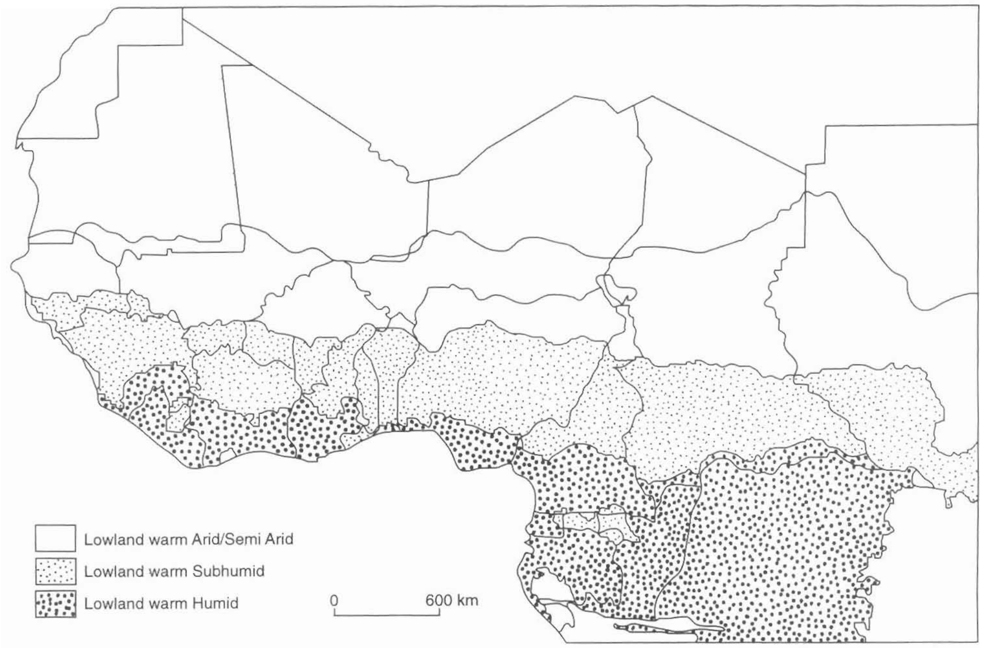

FIG. 1. West and Central Africa showing the lowland warm, subhumid zone where the length of the growing season is between 151 and 270 days and where moist savannas are found. (Extracted from a map of the agroecological zones of Africa by the International Institute of Tropical Agriculture, Ibadan.)

N stocks in wood and other compartments and their flows have not been reported. Bate (1981) has discussed nitrogen cycling extensively in savanna ecosystems, but with a bias towards southern African savannas which are different from West African savannas because they are on higher elevation and have a generally drier climate. One of the most intensively studied of the southern African savannas is the Nylsvley Nature Reserve in South Africa, which has an annual rainfall of 630 mm and a mean annual temperature of 18.6° C (see Table 1 for comparisons). Frost (1985) has reported on the pools of nitrogen and other major nutrients in the Reserve. Abbadie (1989) reports on nitrogen cycling through the herbaceous stratum in the moist Lamto savanna of Cote d'Ivoire, an area of similar physical and bioclimatic features as the wettest sites used for the present study (see UNESCO, 1979: 511). Finally, Robert-

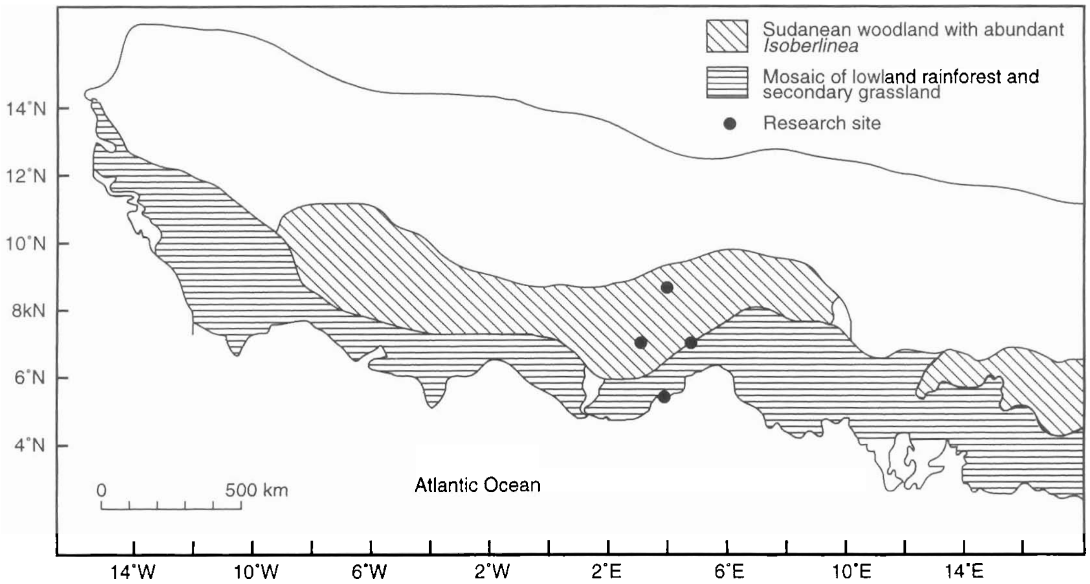

FIG. 2. The moist savanna zones of West Africa (from White, 1983).

TABLE 1. Climatic, soil and vegetation characteristics of the three study sites from which data were collected for compiling nitrogen stocks in Nigerian moist savanna (N = nitrogen, g.b.h. = girth at breast height).

Attribute	South plots	Middle plot (open)	Northern plots
1. Climate			
a. Annual rainfall, mm	1232	1285	1066
b. Rain days yr^{-1}	107	109	85
c. Mean max. temp. (°C)	29	32.33	34
d. Mean min. temp. (°C)	21.67	20.82	21
2. Soil			
a. Parent material	Basement complex	Basement complex	Undifferentiated basement complex
b. Soil type	Tropical ferruginous	Tropical ferruginous	Tropical ferruginous
c. % organic carbon:			
0–15 cm depth	Open savanna: 1.06 Woodland: 1.11	0.72	Open savanna: 0.55 Woodland: 0.51
30–45 cm depth	Open savanna: 0.77 Woodland: 0.91	0.65	Open savanna: 0.57 Woodland: 0.66
d. % nitrogen:			
0–15 cm	Open savanna: 0.07 Woodland: 0.08	0.06	Open savanna: 0.05 Woodland: 0.06
30–45 cm	Open savanna: 0.06 Woodland: 0.05	0.04	Open savanna: 0.04 Woodland: 0.05
e. Soil pH (0–15 cm)	Open savanna: 6.53 Woodland: 6.29	6.29	Open savanna: 6.05 Woodland: 6.34
3. Vegetation			
a. Tree density (trees ≥ 30 cm g.b.h.)	Open savanna: 980 ha^{-1} Woodland: 2375 ha^{-1}	460 ha^{-1}	Open: 233 ha^{-1} Woodland: 261 ha^{-1}
b. Estimated amount of wood, g m^{-2}	Open savanna: 4721 Woodland: 14936	4292	Open: 1030 Woodland: 5493
c. %N of wood cores	0.21 (highly variable)	0.21 (highly variable)	0.21 (highly variable)
d. Mean annual litter fall g m^{-2}	Open: leaf: 62.83 wood: 936.95 Woodland: leaf: 316.79 wood: 223.07	leaf: 118.21 wood: 671.87	Open: leaf: 148.19 wood: 69.65 Woodland: leaf: 240.66 wood: 175.89
e. Mean % N in litter	Open: 0.95 Woodland: 0.97	1.22	Open: 0.81 Woodland: 0.97
f. Mean maximum herb. crop (3 yr) g m^{-2}	Open: 495.58 Woodland: 400.50	331.15	Open: 323.62 Woodland: 258.72
f. % non-grass herbs (3 yr)	Open: 0.46 Woodland: 0.56	0.50	Open: 0.39 Woodland: 0.40
g. Mean % herb. standing crop burned (3 yr)	Open: 96 Woodland: 84	85	Open: 87 Woodland: 73
h. Mean % N in herbs (3 yr)	Open: 0.46 Woodland: 0.56	0.50	Open: 0.39 Woodland: 0.40
i. Mean N loss from burning herbs g m^{-2}	Open: 0.74 Woodland: 0.96	0.88	Open: 0.88 Woodland: 0.78
j. Mean loss from litter burning (g N m^{-2})	Open: 0.34 Woodland: 0.69	0.39	Open: 0.25 Woodland: 0.50

Expanded from Isichei (1983).

son & Rosswall (1986) have discussed the regional cycle of nitrogen in the whole of West Africa.

MATERIALS AND METHODS

Study sites

Data were collected from sites which, according to the zonation of White (1983), are in the Guinea–Congolian mosaic of lowland rain forest and secondary grassland (drier type); mosaic of lowland rain forest, *Isoberlinia* woodland and secondary grassland; and Sudanian woodland with abundant *Isoberlinia*, respectively (Fig. 2). The wettest savanna sites are located within the Olokemeji Forest Reserve (7° 25′ N, 3° 32′ E) (Fig. 2) in two tall *Andropogoneae* savanna fire experiment plots burned annually since 1929. The plot burned late in the dry season (March) has very few trees and is 'open' while the early (December) burned one has more trees and could be described as savanna woodland.

The middle site, located in the Old Oyo Forest Reserve near Igbeti (8° 40′ N, 4° 10′ E) is 'open' and has been described by Keay (1947). The two northernmost (driest) sites are located within the Kainji Lake National Park (10°

N, 4° E) which has been described by Howell (1968). One of these sites is an open *Terminalia avicennioides–Burkea africana–Detarium microcarpum* savanna. The other is an *Isoberlinia* spp.–*Afzelia africana* woodland. The major physical and biological attributes of the sites are listed in Table 1. For convenience, the three open savanna sites are grouped as one and the two woodland sites as another. The data for this study were collected between 1975 and 1980 but it is pertinent to point out that subsequent studies have shown that the sites, being located in reserves where access is restricted, have not changed significantly.

Data collection

Above-ground vegetation and soil. Grass samples were collected at peak standing crop in November in randomly placed 0.25 m^2 quadrats. The herbaceous materials collected were sorted into species and after drying and weighing were analysed for total nitrogen by the Kjeldahl method. Soil samples, up to 45 cm depth, were collected using a bucket auger and also analysed for total nitrogen. The results were used to estimate the amounts of nitrogen contained in g m^{-2} of surface up to the 45-cm depth. Litter samples were also periodically collected from permanent litter traps from which annual means were estimated. The litter was sorted into leaves, fruits/inflorescence and wood, and then dried and weighed and analysed for nitrogen. The nitrogen content of live wood was estimated by analysing wood cores obtained from main stems using a borer.

Herbaceous below-ground biomass. Three to five whole plants of each of the major grasses in the study sites were carefully dug to a 20-cm depth at peak standing crop in October/November. The below-ground portion of each specimen was cut off at soil level, washed, dried and weighed and dry matter ratios obtained. The ratio ranged from 0.44 in the wettest sites to 0.55 in the driest site. Caesar & Menaut (1974) reported a range of 0.33 to 1.05 with a mean of 0.66 at peak biomass for seven savanna formations in Cote d'Ivoire (see also UNESCO, 1979: 539). Non-grass herbs (forbs) constitute a very small portion of the herbaceous stratum in the plots (Table 1).

The below-ground parts of the grass samples were dried, weighed and analysed for total nitrogen while the ratios obtained were used to obtain below-ground biomass for the whole-plot herbaceous biomass.

Estimation of above-ground wood volume. Since the study sites are located in Reserves, destructive sampling of trees was not possible so an indirect method of estimating wood volume had to be used. Coloured 35 mm photographs of identified trees were taken at the two Northern Guinea sites using a Leicaflex camera mounted on a tripod such that the lens centre was 156 cm from the ground and either 18 m or 24.5 m from the base of the tree. Two photographs, taken 90° apart ('frontal' and 'side' views) were taken of each specimen tree. A total of thirty-five trees of fourteen species was photographed. The girth of each specimen tree was measured at 140 cm height and the point of measurement marked before photographing.

The photographic slides of the trees were then each projected at 3.30 m distance on white paper. The diameter at the marked girth point was measured (cm) in the projected slide. This measurement from the photograph was regressed against the field girth measurements. The resulting equation was:

Y (photo diameter measurement, cm) = $-0.0041 + 0.0197X$ (cm girth, field measurement); $r^2 = 0.98$, $n = 35$.

The second step in using the photograph projections in determining wood volume was to divide the entire image of the tree into small, straight segments of nearly equal diameter so that volume could be estimated by the conventional equation: $V = \pi r^2 h$, where r is the radius of the measured segment and h is its length. On average, seventeen segments were required for the measurement of the volume of each image. The means of the total volume estimates made from the two images of each tree were then regressed against the field measured girth to give the equation:

$$\log_{10} \text{volume } (m^3) = 4.4213 + 2.8144 \log_{10} \text{girth (cm)}/\pi$$

As an approximate check, this equation was used to estimate the volume of randomly taken girths (2.54 cm/1 inch) of trees in Table 1 of the work of Odum & Jordan (1970). The natural logarithm of the present estimates was regressed against the natural log of their estimates obtained from destructive sampling. The resulting equation was:

$\log Y$ (present estimate) = $1.0083 + 0.9203 \log X$ (their estimate); $r^2 = 0.97$, $n = 35$.

Wood volume was estimated at the middle and northern sites by randomly laying three 5 m × 50 m transects in each plot and measuring the g.b.h. of every woody plant within the transect. Those < 135 cm high had their heights and midpoint girths measured. Wood volume for trees was estimated using the equation above while the volumes of stumps and woody plants < 135 cm was estimated as for cylinders. Volumes were estimated per tree and then totalled for each plot. Total tree enumerations and girth measurements were available for the southern plots (courtesy of the Forestry Research Institute of Nigeria, Ibadan) and these were used for wood volume estimations.

Wood weights were obtained by taking the dry weights of sample wood cores of known volumes and extrapolating to the estimated volumes.

To estimate the amount of nitrogen in wood, cores were taken from sample trees and analysed for total nitrogen. No cores, however, were taken from tree roots and it was assumed that the N concentration in tree roots were the same as in stems which were analysed.

Below-ground woody biomass. No measurements were made of below-ground woody biomass. For the present study the value of 0.37 has been assumed for the ratio of above-ground wood to below-ground wood in open savanna sites and 0.45 for woodland sites (values obtained for similar savanna formations in Cote d'Ivoire by Cesar &

Menaut, 1974). To strive towards obtaining a more complete picture of the N stocks in the systems under study, some assumptions were made, as follows.

1. A 75% annual turnover of herbaceous roots is assumed. Most roots die during the dry season and root growth is restricted due to water shortage and hard soil during the period (UNESCO, 1979: 537).
2. Animals, with the exception of termites, play a minimal role in N cycling in the savanna ecosystems studied. The density of wildlife in West African savannas is generally very low (Anadu, 1982, Ayeni, 1982). The role of termites, however, was not investigated in this study.
3. Nitrogen inputs into the savanna from rainfall and biological fixation were obtained from the literature (Jones & Bromfield, 1970; Sanogho, Sasson & Renaut, 1980). A figure of 0.4 g m^{-2} is assumed in each case.
4. An annual mineralization rate of 4% of soil total nitrogen is assumed (Jones & Wild, 1975).

RESULTS AND DISCUSSION

Stocks and flows of nitrogen

The stocks and flows of nitrogen in the two types of savanna ecosystems are shown in Figs 3 and 4. The bulk of the nitrogen is in the soil with the woody biomass containing about one-sixth of the soil amount and the herbaceous vegetation much less. In the woodland-type savanna the soil holds 325 g m^{-2} nitrogen to a depth of 45 cm (Fig. 3). Of this amount 13.60 g m^{-2} is available annually for uptake by plants, assuming 4% mineralization. The trees and shrubs absorb 6.80 g, of which 3.63 g is returned to the soil by way of litter while the rest is retained in the biomass. Less than 1 g m^{-2} (0.74) is lost through savanna burning. The herbaceous biomass absorbs 2.43 g N m^{-2} yr^{-1} of which 1.02 g m^{-2} yr^{-1} is returned to the soil by way of litter. 1.00 g m^{-2} is lost from the herbaceous biomass both as standing crop and litter.

In the open savanna (Fig. 4) the soil holds 326 g N m^{-2} in the top 45 cm. If 4% mineralization rate is assumed, then 13.60 g m^{-2} will be available annually for uptake by plants. Estimated uptake by herbs is 2.26 g m^{-2} and 2.18 g m^{-2} yr^{-1} by trees and shrubs. The standing crop of trees and shrubs has 15.92 g m^{-2} N of which 5.04 g m^{-2} yr^{-1} is shed as litter. Nitrogen returned to the soil by way of litter decomposition is 1.84 g m^{-2} yr^{-1}. A further 0.63 g m^{-2} is lost when litter is burned in open savanna.

The herbaceous biomass absorbs 2.26 g N m^{-2} yr^{-1}, of which 1.11 g is returned to the soil by way of litter decomposition; 0.73 g is lost annually when the herbaceous biomass is burned.

The values of nitrogen stocks in soil and the various vegetation compartments are close to those reported by Abbadie (1989) who worked in the Lamto savanna of Cote d'Ivoire. Comparisons of his work and that of others in savannas are presented in Table 2. Bate (1981) reported

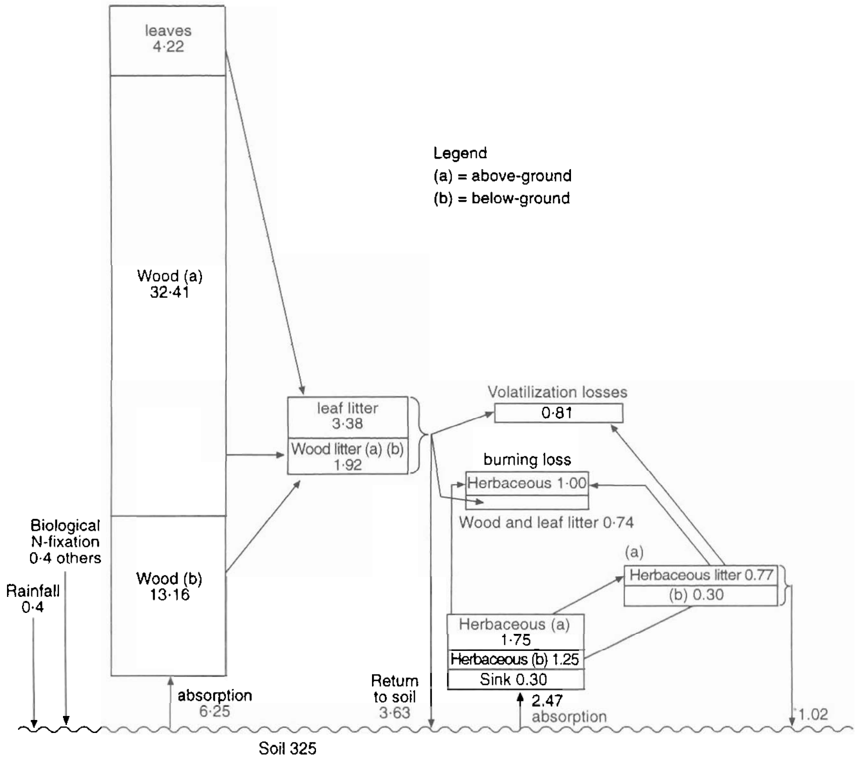

FIG. 3. Scaled compartmental stocks and flows of nitrogen in vegetation and soil in moist savanna woodland, Nigeria. Stocks and flows are in g N m^{-2} yr^{-1}.

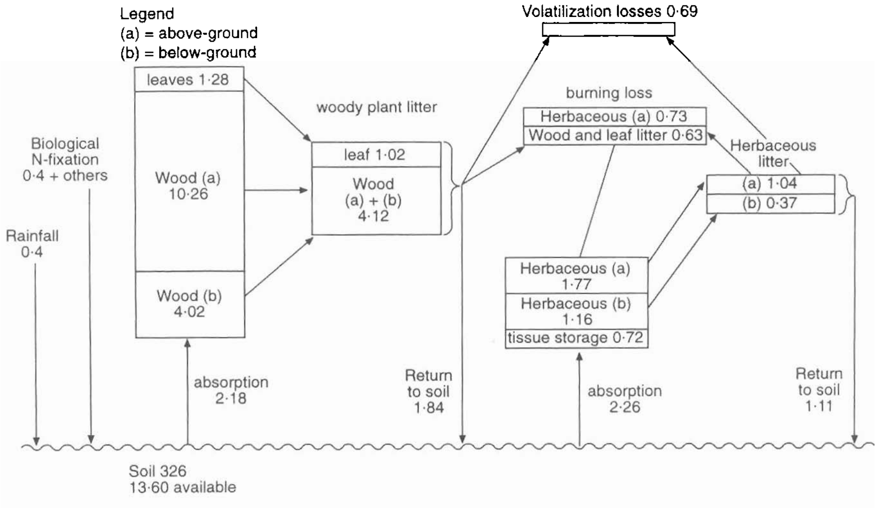

FIG. 4. Scaled compartmental stocks and flows of nitrogen in vegetation and soil in moist open savanna, Nigeria. Stocks and flows are in g N m^{-2} yr^{-1}.

total biomass nitrogen in southern African savanna to be 14.5 g m^{-2} (145 kg ha^{-1}) for the woody component and 0.5 g for the grass component. Total soil N to the average depth of 1 m was approximately 330 g m^{-2}.

The results obtained in this study could be useful in the assessment of the effects of global change on savanna ecosystems. It has been observed that increase in carbon dioxide levels may not necessarily lead to increase in carbon accumulation unless there is an increase in C:N ratio (Rastetter *et al.*, 1992). Furthermore, Bate (1981) has observed that mineralization rates limit the supply of N in savannas, microbial activity being limited by lack of assimilable carbon. Climate change could affect nutrient cycling and structure of savannas in several other ways. First, savanna is essentially a tree–grass combination with most of the grasses being C4 and the trees C3. Moist savannas have a considerable amount of forbs (see Muoghalu and Isichei 1991) which are most likely C3. Under conditions of elevated CO_2, C3 plants show larger responses (higher productivity). This means that trees and forbs will increase more rapidly than grasses. This might mean more nitrogen in the herbaceous layer and therefore more rapid recycling due to faster turnover of herbs. Plants grown with supplemented CO_2 have been reported to show a five-fold increase in N-fixation compared with untreated controls (Kristiansen, 1993). Leguminous forbs fix atmospheric nitrogen symbiotically but nitrogen is also fixed in the rhizosphere of grasses. Overall, forbs should be at advantage because they fix at faster rates.

With increasing atmospheric carbon dioxide levels plants allocate proportionally more carbon below ground than above ground, causing an increase in root:shoot ratios. Abbadie *et al.* (1992) have observed that most of the nitrogen assimilated in savanna originates from the decay

TABLE 2. Comparisons of the nitrogen stocks in moist savanna with results obtained from various studies of nitrogen stocks in similar savanna formations.

Study reference	Soil nitrogen g m^{-2}	N in above-ground herbaceous vegetation	N in above-ground woody vegetation	N in below-ground woody vegetation
Present study	326, 325 (0–45 cm)	1.77, 1.75	11.82, 36.63	4.02, 13.16
Abbadie (1989), Lamto:	(0–50 cm)			
Loudetia simplex	276.0	— (Not measured)	—	—
Andropogoneae	289.5			
Unburnt savanna	311.8			
Singh & Yadava (1974), Indian grassland	—	0.20–3.484	—	—
Frost (1985), *Burkea* savanna	365.4 (0–100 cm)	2.02	13.9	7.64
Bate (1981), estimates for *Burkea* savanna	330 (0–100 cm)	0.5	14.5	—

of root litter, mineralization rates of soil organic matter being low and biological N fixation and contributions from bulk precipitation being minimal. High CO_2 can also increase the number of branches, tillers, flowers or fruits in a plant. Trees and herbs are likely to be equally affected in this respect. Carbon and nitrogen dynamics have received significant attention in global change modelling (e.g. Parton *et al.*, 1993). This study could add to the savanna modelling data base and improve predictions of the effects of global change.

It has been observed that elevated CO_2 levels lead to early maturation in annuals and delayed leaf senescence. It might thus appear that the frequency of fires in moist savannas will reduce (low dry dry-season fuel) but fire intensity and consequences of such aperiodic events will increase under a changed climate. This has implications for global climate because of the expected increased emissions from burning and also the attendant effects on savanna structure.

Land use changes affect vegetation structure and nutrient cycling and in moist savannas such changes are usually brought about primarily by slash and burn agriculture. The end result is a reduction in tree density and when further overgrazed, forbs take over from grasses in the savanna herbaceous layer. Thus, land use changes and global change will result in roughly the same type of landscape in moist savannas with reduced nitrogen and carbon stocks.

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